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Symposium on "The Life Cycle in Insects."¹*

1. APTERYGOTA.

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In a discussion of the life cycles of insects it is logical to begin with Apterygota because their type of life cycle is the simplest, as it involves no metamorphosis.

Though Thysanura and Collembola undergo no changes that are sufficiently striking to constitute a metamorphosis, they nevertheless exhibit in their postembryonic development various minor changes of structure and coloration.

For example, *Lepisma saccharina* at hatching is whitish; is a slender creature, on account of its narrow thoracic segments; and does not have as yet the characteristic styli of the eighth and ninth abdominal segments. The antennæ have only 22 segments, though they later develop some 60 or 70 subsegments; and the lateral cerci have at first only 10 segments. *Lepisma*, as it emerges from the egg, has no scales. Even the first molt, which occurs seven days from the time of hatching, brings no change in these respects. (Heymons.)

In Collembola, at hatching, the head is large in proportion to the body—much as in a grasshopper. As the individual grows there are changes in the relative lengths of the segments of the body and of those of the appendages. Thus, in *Tomocerus vulgaris*, comparing small and large individuals:

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	SMALL	LARGE
Ratio, third to fourth antennal segment.....	1:1	2.9:1
Ratio, third to fourth abdominal segment.....	1:1	1.5:1
Number of intermediate teeth of mucro.....	1	8
Number of teeth of unguis.....	1	4 to 6

Intergradations in these respects occur in individuals intermediate between these two extremes. This variation, occurring during the growth of a single individual, is so extensive that one who studied only one of the youngest and one of the oldest specimens might easily mistake them for two distinct species. (Schäffer.)

In a few Collembola the number of antennal segments increases after birth. *Heteromurus*, for example, is born with four, but develops five by the division of the basal segment into two. *Orchesella* has at first four, and finally six, by the division of the two proximal segments. The fourth antennal segment may become subsegmented after birth, as in *Sminthurus* and *Heteromurus*; and numerous subsegments develop in the third and fourth segments in *Tomocerus*.

The postembryonic changes in coloration in Collembola are often striking. Collembola at hatching are usually white (sometimes yellow), except for the black ocular pigment, though most of them acquire pigments and color patterns later. *Anurida maritima* at first white, becomes dark blue. Species of *Sira* at birth lack their characteristic color patterns. *Calistella*, yellow at hatching, gradually develops its color pattern with each molt, and completes its pattern with the seventh molt. (Skorikow.)

Our knowledge in regard to seasonal histories in Apterygota is fragmentary. *Campodea fragilis* survives the winter and has been kept alive several months in captivity. *Machilis maritima* lives longer than one year, is sexually mature in spring, and does not molt in winter but molts at frequent intervals during the rest of the year. *Lepisma saccharina* is like *Machilis* in these respects. (Oudemans.)

Among Collembola, *Achorutes armatus* in Massachusetts has three generations during the year, and possibly four, which mature at intervals of about six weeks. *Achorutes packardi* in Massachusetts has two broods annually, the eggs being laid late in April and hatching in about one month. This species exhibits seasonal dimorphism; its variety *dentatus* laying eggs that produce *packardi*.

The following data were sent to me from Arnprior, Ontario, by Mr. Charles Macnamara, an exceptionally keen and thorough observer:

"Around here *Achorutes socialis* (the 'snow-flea') oviposits in spring, and the mature individuals have disappeared completely by June 1st. Well-grown individuals begin to appear again in September and October, but the very largest usually (not always) are to be found only in April and May. Apparently they grow all winter under the snow. As an exception though, I found some 2 mm. individuals (the maximum size) in late October, on a white birch.

"Eggs of *Achorutes socialis* hatch in 11 to 14 days, and in 9 to 10 weeks the young are .3 mm. to .5 mm. long, and fairly well pigmented. Another spring layer is *Onychiurus simetarius*; eggs of which laid May 2, hatched May 22, period, 20 days.

"In my vials in the house, *Achorutes humi* and *Neanura muscorum* both oviposited in the early winter. Eggs of *A. humi* laid November 15, hatched December 7, period, 22 days. Those of *N. muscorum* laid December 4, hatched January 8, period 35 days. Under natural conditions outside, however, I doubt if the eggs of these two species would have hatched until spring.

"Specimens collected as well-grown adults survive in captivity for very various periods. *Sminthurus* and *Papirus* in my hands are always very short-lived—a few weeks at most. *Isotoma* may live for a couple of months, but the most resistant to captivity are *Achorutes socialis*, 5 to 6 months; *A. packardi*, 7 months; and *Xenylla maritima*, 12½ months. In estimating the length of life to these periods should be added the age when captured, and of course that is unknown to me.

"*Achorutes socialis* continues to grow long after it is sexually mature, and keeps casting its skin as long as it lives."

This is true of Collembola as a rule, which molt after growth has ceased. The total number of molts has not been ascertained in the case of any collembolan. *Tomocerus plumbeus* molts throughout the year at intervals of two to three weeks. (Sommer.) In *Tomocerus flavescens americanus* the intervals between successive molts increase with the age of the individual. Thus the youngest specimens molt every two days, and old individuals every six to eight days.

It remains to summarize the significance of these facts as follows: Apterygota at hatching are not structurally finished, or complete; but undergo further development in respect to various details of structure.

The postembryonic development of pigmentation in Collembola is (to judge from observations made on several genera) the direct result of exposure to sunlight, and may be prevented

by keeping the insect in darkness, as in the case of *Anurida*. On the other hand, the embryo *Anurida* develops pigment prematurely if the egg is exposed to sunlight.

The colors and color patterns of *Collembola* are not known to have any adaptive significance. Many *Collembola* resemble their environment in color, to be sure, but there is no evidence that this resemblance is of any advantage to the organism.

The most conspicuous fact in regard to the seasonal history of *Collembola* is their tolerance of low temperatures. Many species are active in winter when most other insects are not. Some species grow and molt during winter, and lay eggs at low temperatures. Thus one species was seen to lay eggs at 0° C. The temperature-range of activity is lower than that of other insects. *Thysanura*, on the contrary, are far less tolerant of cold. Some of them hibernate but do not grow, molt, or lay eggs in winter. *Thysanura* are not known in the Arctic region; though the arctic and subarctic *Collembola* number some seventy species.

Apterygota molt at frequent intervals throughout life; are long-lived and have therefore many molts; the number being indefinite.

In *Collembola*, ecdysis is something more than a provision for growth; occurring as it does after growth has ceased; and being, in part at least, an excretory process. With each molt the inner half of the epithelium of the mid-intestine is cast off and discharged from the food canal, and with it are expelled pseudocrystals of sodium urate, which have previously accumulated in the epithelial cells. This process is correlated with the absence of Malpighian tubes in *Collembola*.

Apterygota best illustrate simplicity of the life cycle. They are relatively simple in structure, development and habits, in correlation with their environment, which is relatively simple and remains constant. The functions of growth and reproduction are not sharply separated as they are in *Pterygota*. *Apterygota*, being primitively wingless insects, show none of the specializations associated with the presence of wings; such as a firm integument, differentiation and consolidation of the thoracic segments, and the development of various thoracic sclerites in relation to muscles of locomotion. Neither are there found such extensive modifications of the abdomen in relation to reproduction, as occur in pterygote insects.

Thysanura and Collembola exhibit certain specializations of structure and function, but these are of minor importance—Apterygota being essentially the most generalized group of insects. They exemplify a life cycle without metamorphosis and are, so to speak, larviform, but with the power of reproduction.

2. THE LIFE CYCLE OF THE ORTHOPTEROID ORDERS.

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The Orthopteroid insects (sens. lat.) include all such forms as have mouth-parts of the mandibulate type and undergo a gradual or "incomplete" metamorphosis.

As in other orders of insects, the extent to which the immature stages ("nymphs") diverge from the adult in form and structure is more or less proportional to the differences in environment and habits. Accordingly they may be divided into two groups, (1) those which are terrestrial throughout life, and (2) those in which the early stages are aquatic.

Group 1 includes the Blattoidea, Mantoidea, Isoptera, Zoraptera, Grylloblattoidea, Phasmoidea, Orthoptera, Dermaptera, Embiidina, Corrodentia and Mallophaga. Group 2 includes the Plecoptera, Ephemerida and Odonata.

In Group 1 the habitat and feeding habits are not materially altered during the life cycle, so that the same structural adaptations are present throughout life, and the metamorphosis is entirely gradual, except at the last moult, when the wings, if present, and the genitalia undergo more or less marked changes. There is, however, little or no histolysis of larval structures. The number of moults is comparatively small, so far as known, being usually four to six, but sometimes reduced to two or increased to seven or eight. A pronymphal stage is sometimes present. The nymphs resemble the adults except in size, details of proportion, chaetotaxy, sculpturing and sometimes colour-pattern, and in the thinner cuticle. The number of antennal and occasionally tarsal joints sometimes increases with growth, and the ocelli, when present, may not appear until the last moult. The wings, when present, appear at an early stage,

usually the third or sometimes the second moult. Primitively they appear as caudo-lateral extensions of the meso- and metanota, from which they become separated at a later stage by a suture and a more constricted base.

The leading features in the life cycles of the orders of Group 1, so far as known, may be summarized as follows:

Blattoidea. Mostly nocturnal, hiding by day, with a tendency to be gregarious: feeding chiefly upon animal and vegetable refuse; eggs (16-50) arranged in two series in a horny ootheca, formed in the uterus, and carried for a time in the genital orifice; dropped in protected places without attachment; period of growth variable, 4 or 5 months to several years, but usually one brood annually; number of moults variable, generally 5-7. Hibernation in egg or nymph state. The adult males of some species differ considerably in form from the nymphs and the adult females. Styli of female disappearing at last moult, usually persistent in the male.

Mantoidea. Diurnal, solitary, living on foliage or on the ground, predaceous on other insects; eggs arranged in several series in a membranous or vesicular ootheca formed at the exit of the genital passage and attached to other objects, the number deposited varying enormously in different species (20-1000); incubation period varying according to season, a few weeks (summer) to 10 months (winter); hatching as a pronymph; number of moults 7 or 8 (Mantis); usually one brood; hibernation in egg or nymphal stages. Styli as in Blattoidea.

Isoptera. Cryptozoic, living in communities, often of many thousands of individuals, which are polymorphic, there being in addition to the fertile adults and nymphs, sterile wingless castes of one or two types (soldiers and workers) and sometimes reserve fertile individuals (substitution royalties), which in other respects remain immature. Reproductive activity limited to few individuals, the kings and queens, (and the substitution royalties), the queens of enormous fecundity, and having the final or reproductive stage greatly prolonged (sometimes several years). Superfluous winged adults leave the colony, flying in swarms, but soon lose their wings. Food largely of wood, proctodeal excreta, saliva and organic refuse, varying in composition according to caste. There are generally no special modifications in the nymphs, except the lack of eyes and

the very thin cuticle, associated with the cryptozoic life. The number of antennal segments increases with development. Large prothoracic expansions are present in the nymphs of some species.

A few species of Isoptera are inquilines in the nests of other species of the same order.

Zoraptera. Inquilines in the nests of certain Isoptera; life cycle unknown.

Grylloblattoidea. The single species is alpine, living under stones and on snow; carnivorous (has been fed on ant pupæ); metamorphosis practically confined to the genitalia; styli present except in adult female. Hibernating as nymph or adult.

Phasmoidea. Phytophagous, generally on trees and bushes; voracious and reaching in some species an enormous size. Eggs few (12-100), each in a separate seed-like capsule, dropped at random. Incubation period sometimes extending over two years. Period of growth variable, 6 weeks to 16 months; number of moults few, variable, two or three in known cases. Nymphs usually not differing much from adults.

Orthoptera. Diurnal or nocturnal; arboreal to subterranean; phytophagous or partly carnivorous. Eggs moderately numerous, buried in plant tissues or in the ground by an ovipositor (except in subterranean forms); in the Acrididæ imbedded in a vesicular ootheca. Incubation period generally over winter in temperate climates, comparatively few species hibernating as nymphs or adults. Generally one brood, moults 4 to 6. An inversion of the wings takes place at about the fourth moult, the hind wings overlapping the front, until the final ecdysis, when the normal position is restored and the hind wings folded. Otherwise the nymphs are usually lacking in special modifications, though the color pattern is sometimes distinctive.

Dermaptera. Carnivorous and phytophagous; eggs dropped at random but sometimes picked up afterwards by female and carried to places of safety; in *Forficula auricularia* deposited in early spring; period of growth in this species about 5 weeks; moults 3 or 4. One or two broods, hibernating at various stages. Special form changes: Increase in the number of antennal segments; cerci of a few primitive genera segmented in the nymphal stages.

The aberrant African genus *Hemimerus*, parasitic on rodents, is viviparous.

Embiidina. Living under damp stones and wood on the ground, nests of ants or termites, in small colonies but not forming societies; the nymphs constructing passages lined with a silk-like secretion from glands in the maxillæ; partly carnivorous, partly phytophagous; nymphs very similar to adults. Tropical or sub-tropical.

Corrodentia. On bark, under logs, old books, etc., feeding on animal and vegetable refuse, mouldy substances, etc. Eggs laid in patches or clusters under bark, or in other protected places, covered with a web; incubation period generally during winter in temperate climates. Period of growth probably short, there being sometimes two or perhaps three broods. Number of moults said to be four in *Psocus*. Nymphs resembling adults but without ocelli, which are present in the adults of winged species.

Mallophaga. Epizoic on birds and mammals, feeding on feathers, epidermal debris, etc.; eggs glued singly to hairs or feathers in the area inhabited by the insect, sometimes localized in groups common to many individuals. Incubation period not known definitely for any species, probably long; number of moults also unknown, apparently few. Length of life probably several months in most cases.

In Group 2 the nymphs, or *naiads*, differ from the adults more widely than in group 1 in correlation with the greater difference in environment. The period of growth is usually longer, being frequently three years, and the number of moults greater. Length of life cycle is to some extent proportional to size attained.

Plecoptera. The stone-flies show least divergence between larval and adult structure. The adults are feeble insects of secretive habits, serving only for the function of reproduction. Eggs small, carried by the female for a time in a mass at the genital orifice, and finally dropped freely into the water. Naiads inhabit well aerated water, clinging to undersides of stones, to which habitat they are adapted by the possession of filamentous tracheal gills, chiefly thoracic, and by their flattened form and legs, the latter fringed with swimming hairs. Food of naiads smaller aquatic animals. Length of life probably one to three years; number of moults not known for any species, probably very variable. Adults appear usually early, sometimes emerging on ice and snow, the order having on the whole a remarkable power of withstanding cold.

Ephemerida. Naiads phytophagous, diverging from the adults more widely than in the Plecoptera and showing a wider range of adaptation in form and structure. Life cycle varying from a few weeks to three years, aquatic except in the last two stages (subimago and imago), both of which have functional wings but live only a few hours to a few days and take no food. Number of moults large, apparently sometimes 30 or more. The most marked changes acquired on reaching the subimago stage are the enlargement of the compound eyes, the development of ocelli, reduction of antennæ and mouth-parts, development of wings and genitalia, loss of the tracheal gills, elongation of the cerci, with loss of their setae, besides more or less marked changes in general form. Adult phase generally appearing in early summer, usually crepuscular or nocturnal and serving only for the mating function. Eggs deposited in large numbers, without capsule, sometimes attached to other objects.

Odonata. The habitats and corresponding modifications of the naiads of this group are similar to those of the preceding, but their habits are wholly predaceous. Developmental period varying from a few months to three years or more, the number of moults variable, even in the same species, 11 to 15 in known cases. A pronymphal stage is present.

The principal adaptations of the naiad are: Modification of the labium as a prehensile arm; (2) special respiratory organs, viz., three leaf-like terminal tracheal gills in the suborder Zygoptera, which also serve as fins, or numerous gills in the rectal chamber in the suborder Anisoptera. Wing pads of naiads reversed in position as in Orthoptera. Adults comparatively long-lived, active, predaceous, diurnal, showing the following changes of structure at the final moult in relation to the change of habits: Enormous enlargement of compound eyes and development of ocelli; shortening and change of form of labium, the larval structure being absorbed by histolysis; modification of thoracic segments and legs in adaptation to habits of flight and perching; elongation of abdomen and development of genitalia. There is a short quiescent stage, equivalent to a pupa, in which no food is taken. Oviposition endophytic or exophytic, the eggs in the latter case being sometimes scattered, sometimes enclosed in a gelatinous envelope, or attached to objects in water; generally several hundred deposited.

3. THE LIFE CYCLE IN HEMIPTERA (*Excl. Aphids and Coccids.*)

By E. D. BALL.

The life history of any insect if carefully and conscientiously traced, will show many and striking adaptations. These in the aggregate will be found to display a marvelous adjustment to and harmony with the environment. The life cycle may be long or short, occurring early or late, the generation one or more and the winter passed as egg, nymph or adult, according as these variations adapt the insect to its individual niche in the scheme of things.

In the main these adaptations are not, however, mere adjustments to a temporary excess of heat or cold, moisture or dryness, but rather are deep-seated and fixed modifications brought about through reaction to seasons unnumbered whose means, at least within the limits of the present geological period, are constants. Such adaptations as these are not to be overthrown by the influence of an early season or a late one, a heavy rainfall, or even an arid condition. They are merely modified in detail, but these modifications only serve to emphasize the fixity of the underlying principle. The man who wrote "The number of generations a year will vary in different parts of the country according to the various climates and is likely to fluctuate from year to year in accordance with seasonal variations" was so impressed with trivial details that he entirely missed the great concept of nature's plan whereby each and every species exists as a species primarily because it has through the ages become differentiated and adapted to its humble place in the structure of life. His concept of nature is that of the thistledown blown by the wind while the reality is the majestic elm bending and waving in every passing breeze but which in the end remains firm and upright.

Commencing with the CICADIDÆ as probably the lowest type of the field assigned, we find a marked uniformity in their life history in that all the species pass the winter as nymphs and all have an under-ground habitat, coming out as adults with marked uniformity in the middle of the summer. Beyond that,

ittle is known except for one species in which the life cycle requires 17 years and a variety in which this number is reduced to 13. Popular opinion credits the other species with two-year cycles. According to W. T. Davis this originated with Jæger in the "Life of North American Insects" published in 1854 and he credits the information to Pontedera. Whether Pontedera's statement was the result of experiment or only a guess has apparently never been tested. Absolute fixity of the 17 and 13 year cycles is, however, one of the marvels of nature and should be an everlasting refutation of any suggestion that insect activity is subject to fluctuation like the ever changing thistledown.

The CERCOPIDÆ or Frog-hoppers show a marvelous adaptation in their froth making habit and they have apparently depended largely upon this rather than other modifications for their protection. All of our local species have a single annual generation and all but one pass the winter in the egg stage. The variations in this single generation will be discussed under that head in the next family.

The MEMBRACIDÆ or tree-hoppers are celebrated for the wonderful variety and complexity of their adaptations to their food plants. When it comes to the life cycle on which most of these adaptations are based, it is found to be fundamentally very simple. 90 per cent or more of our species have a single annual generation and more than 90 per cent pass the winter in the egg stage. The tree hoppers of the genus *Telamona*, for example, feed very largely on the sap of the trees and mainly on the tender growing twigs. They find optimum conditions for such feeding only during the comparatively short period in which the tree is making its growth. They also must find a location and deposit their eggs while the wood is still soft and tender; otherwise they will be unable to penetrate to a sufficient depth to protect the eggs from predacious and parasitic insects. The result is that we find that they, with a possible exception, pass the winter in the egg stage and have a single annual generation. The overwintering eggs in the twigs hatch almost with the first growth in May. The nymphs mature in June. The adults lay eggs in July and August and the cycle is finished.

In the case of *Ceresa bubalis* (the Buffalo tree-hopper) and its vegetation-feeding allies the need of haste is not so great as their food plants, Compositæ, Legumes and others, grow all

summer, so we find the nymphal period both longer and later and the adults extending into the fall.

A striking adaptation to a special period in a plant's growth, is shown in the life cycle of *Micrutalis calva*, the little shining black seed-like tree-hopper. The nymphs are found between the branches of the blossom head of the Ironweed, *Vernonia*. This purple flower appears only in the fall, so that the single generation of nymphs comes on over 70 days later than its relative that lives in the tree.

Later appearing nymphs usually come from overwintering adults that feed for some time before laying eggs. The complete life cycle of this species is not known. What we do know corresponds with the life cycle of *Publilia* in which we know that the adults hibernate and that there is a single generation on thistles, sunflowers and other late growing *Compositæ*.

The writer has never studied a double brooded tree hopper. Funkhouser, a careful student of the family, has, however, published the details of his observations on *Vanduzea arcuata* which lives on the Black Locust. From the observed facts the writer has been able to construct a complete life history chart showing two generations, with the winter passed in the egg stage.

It is to be regretted that after completing this fine series of observations that Prof. Funkhouser allowed himself to be led astray by the example of that all-too-numerous band of dilettante and superficial workers in Entomology whose chief indoor sport has been the working out of life histories by the mathematical route. The only thing necessary for these scientific wizards is to ascertain the time that it takes an egg to hatch and a nymph to develop, add the two, and divide the length of the season by this number. The quotient is *not* the number of generations nor even the number of *possible* generations of the insect that they fondly imagine it to be, but a mathematical fiasco and a scientific absurdity, patent to anyone who will give the matter serious thought.

If the time of the stages used was a fair average of the season our short-cut investigator will probably find three or four broods. If the minimum time found in the midsummer period alone is used and our rapid calculator is optimistic about the spring and fall weather, as he is usually, then at least 5 or 6 generations will be proclaimed. If our mathematical prodigy would only take the trouble to investigate the literature (which

he will not) he would find that no one has ever carried a single species of the higher Homoptera through as many as three complete generations in a season.

There are two fundamental fallacies embodied in all calculations of this kind. The first and most important being that Nature is trying to see how many generations she can produce annually. She is not—in Hemiptera or Orthoptera at least—but rather trying to see how perfectly she can adjust the distribution of the one or two generations to the optimum conditions for development in the variable seasons. The tree hopper might have three generations as far as the time factor was concerned but it can have tender twigs for only one and one it consequently has. The little black *calva* might have three and our mathematical optimist would say four generations but it could not have the rich food destined for the forming seeds in more than one and so it is content with one.

The second common fallacy is that the time from egg to adult is the measure of a generation—it is instead only about half of the period. In the Hemiptera the adult emerges with eggs undeveloped and they must feed and develop them before egg laying begins. Somewhere in this period mating takes place. Funkhouser shows mating 10 or 15 days after the adults appear in *Vanduzea*. Johnson states that the grape leafhopper fed 10 days before mating, Childs shows a longer period for the rose leafhopper, while Fenton and Hartzell show a still longer period for the potato leafhopper before egg laying began. In some cases the mating appears to be near the beginning and in other cases near the end of the period, but in all cases it must of course precede egg laying. The total time therefore between adult emergence and egg laying appears to be from 10 to 25 days.

Hemipterous insects rarely if ever lay all their eggs at one time. Instead the Homoptera as a rule lay a few at a time through long periods. Hodgkiss found *Stictocephala* laying as many as 250 eggs through a two-month period. Johnson found the grape leafhopper laying 115–140 eggs through a 70-day period. Ball found the beet leafhopper laying eggs for two and a half months. Fenton and Hartzell found the potato leafhopper laying eggs for 50 days. In all life history studies made, this period has been shown to be longer than the time required from egg to adult and often two or more times as long. This period,

which must be considered as part of the time required for a complete cycle, will amount to from 30 to 70 or more days.

The total time required for the development of a complete generation of a Hemipterous insect will then be made up of the following factors and be somewhere within the limits suggested:

	Min.	Ave.	Max.
Development of eggs (including mating time).....	10	17	25
Period of egg deposition.....	30	50	75
Egg Stage.....	10	15	35
Nymph stage.....	12	30	55
	62	112	190

This tabulation, which is of course merely suggestive, indicates that the minimum time necessary to mature a complete brood is over two months, the average time three and two-thirds months, and that in some cases it requires over six months for the process.

With these facts in mind we may return to Professor Funkhouser's too ready acceptance of the facilities of the mathematical prognosticator and note that the first two of his proposed generations correspond with the beginning and maximum of the first generation according to his own statements and that the remaining two belong in the same way to the second. He found only two mating periods and these correctly.

Wildermuth working in Tempe, Arizona, gave careful and accurate figures on the beginnings of each stage in the life cycle of *Stictocephala festina* and especially increased our knowledge of the effect of temperature upon the rate of development of eggs and nymphs, showing an average variation in egg development from 14 to 35 days and of nymphs for 32 to 68 days. He, however, was led into the common error and after giving detailed figures enabling the writer to chart two definite broods he "calculated" that there were four broods. He did not give figures that would enable one to close up the posterior extensions of the stages with accuracy but the ordinary extension is amply sufficient to explain the presence of all stages late in the season which misled him into the four brood fallacy. The chart is also interesting in showing the wide variations in the time of appearance of insect life in the arid southwest as compared to that in New York. This is especially noticeable when it is remembered that this is a species with an adult hibernation which under

ordinary circumstances would tend to throw the first generation later than the one that wintered in the egg stage.

The writer's experience in the arid region and especially in the Imperial Valley indicates that this early starting is an almost uniform adaptation. Insects develop abnormally early in the spring before ordinary temperatures are reached and their life cycle is practically completed before the drying up of the vegetation by the excessive heat of the fall so that only those stages that are developed to resist adverse conditions remain in any numbers. This will be brought out again in the case of the grape leafhopper.

The CICADELLIDÆ or leafhoppers, have more economic species and have received more study than any other family in the group. On the other hand the FULGORIDÆ, called lantern flies, or more commonly leafhoppers have probably received less attention. Both groups of these leafhoppers appear to have about the same variation in their life cycles and will be treated together. These leafhoppers feed on all types of vegetation, trees, shrubs, perennials, biennials, and annuals, under every condition of humidity, moisture, and temperature, and yet the writer has never been able to find a single example in which it could be demonstrated that more than two generations a year occurred nor on the other hand one in which there was less than one generation per season. This is a very limited range and yet, in almost every case investigated, a definite and sufficient reason could be found for the limitation in generations and that reason was almost invariably its adaptation to some period in the growth of its food plant.

The leafhoppers with a single annual generation may be roughly divided into three groups, depending upon whether they pass the winter as eggs, nymphs or adults. In general passing the winter in the egg stage will result in the earliest development in the spring, and in this class we find *Empoasca unicolor*, the real apple leafhopper. This species has been worked out by Lathrop in New York, Brittain, in Nova Scotia, and Fenton in Iowa, and all of them find an early nymphal period in May and June, with adults from that time on throughout the season, egg laying occurring late and these eggs going over winter. This, as explained previously, is the adaptation to the short period of growth of the mature apple tree and is a general type of adapta-

tion found in a large number of tree-infesting leafhoppers such as those found in the family *Bythoscopidae*.

But a small percentage of the leafhoppers winter in the nymphal stage and when they do it is usually in response to some peculiar adaptation. *Dorycephalus platyrhynchus*, is a remarkable shovel-nosed leafhopper so wonderfully fitted to the stem of the *Elymus* (wild rye), that it is even said to show the rust spots so well that the species of rust can be determined. This species shows an equally remarkable adaptation in its life history. The eggs which are laid through a long period of time, hatch out at the time the flowers appear, and the little alligator-like hoppers waddle their way up the stalk to the head and come to rest flattened out beneath the glumes where they remain and suck out the nutrition intended for the developing seeds. When the seeds mature they pass to the base of the plant and feed on the green sprouts until winter. In the spring they come out and feed again until May when they change to adults, ten or eleven months from the time they left the egg. It would take a mathematician of some ability to figure many generations in a season of this species and it would take a mind of equal ingenuity to devise a more interesting adaptation.

In the old group *Tettigonidae* the great majority of the species pass the winter in the adult stage and have a single annual generation. *Oncometopia lateralis* is a typical example of this group. In this we see the adults mating and beginning laying eggs in May, continuing until the end of July. The first eggs develop into adults some time before the last of the overwintering brood of adults disappear so that we have adults the year round and nymphs coming on through a period of three or even four or more months. The writer studied this species in Colorado and there the adults that develop, whether early or late, do not become sexually mature until the winter has been passed. The continuous occurrence through such a long period of time has frequently led the mathematical investigator astray. Sanderson working in Texas suggested a possible five generations, while Gibson working in Arizona, with what was probably a two brooded species, announced six.

Turning to the two brooded species of leafhoppers the life history of *Empoa rosea*, the rose leafhopper, was carefully worked out by Childs in Oregon and shows a beautiful adaptation to the long and even temperature conditions during the growing season

of that region. Starting as early as the first leaves appear this species has a generation on rose the adults of which fly to the apple, producing there a second brood which in turn flies back to the rose to deposit eggs to pass the winter.

In sharp contrast with this extended life history period the potato leafhopper *Empoasca malii* as worked out by Lathrop in New York and Fenton and Hartzell in Iowa, shows a very restricted developmental period. The adults hibernate and as usual with such species appear late in the spring, feed on weeds through May, and fly to the potatoes in June. This year they appeared suddenly on potato June 6th, where they laid eggs for nearly two months. The first generation was produced on the early potatoes but the adults did not lay eggs there as they appeared. Instead they waited until after the summer migration which was mostly to the late potatoes and deposited their eggs there for a second generation in the fall. Adults of this generation did not become sexually mature that season. The two periods of development of hopperburn coincided with the development period of the two generations of nymphs. This species has previously been credited with four generations in Minnesota, five in Iowa, while one enthusiast, not to be outdone, announced six for Mississippi, although there is not a single suggestion that any continuous breeding work from generation to generation had been done to verify these preposterous statements. By reference to the charts it will be seen that there would be adults, eggs, and nymphs present on the vines in numbers continuously from the middle of June until frost and this was apparently the only justification for the use of the mathematical method.

The most carefully worked out study of the life history of a leafhopper ever published was made by Fred Johnson on the shores of Lake Erie in 1912. Johnson succeeded in keeping the grape leafhopper, which winters as an adult, alive in cages through the summer and on into September and obtained from 115 to 140 eggs apiece deposited through a period of more than 60 days. He found a single complete generation of nymphs extending from June to October, a period long enough so that three individuals could have successfully matured. Only the very earliest adults of the developing brood appearing in July ever mated and the resulting production of nymphs of a partial second generation was so small as to be almost negligible. Con-

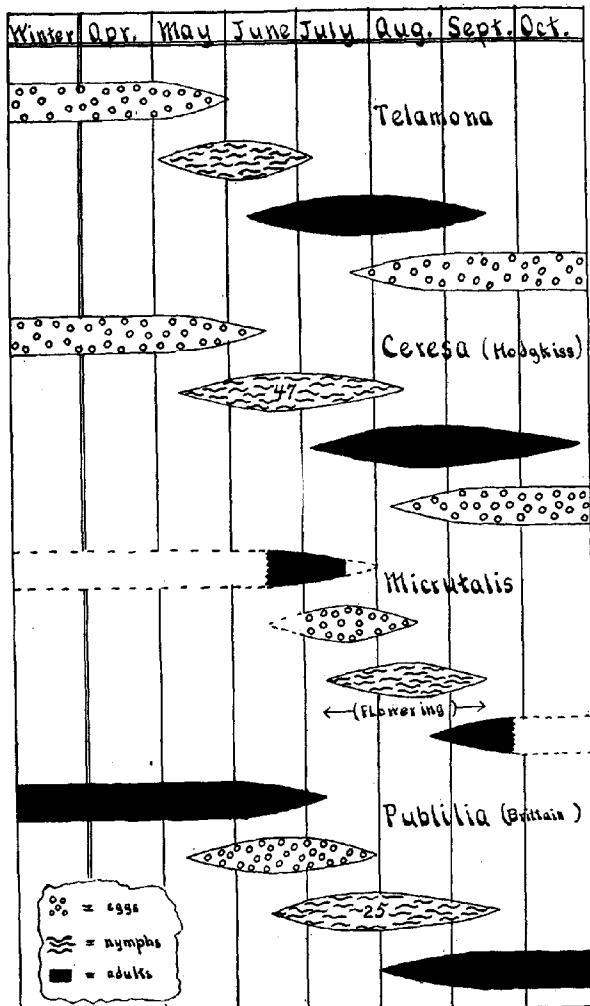
trasting with this Quayle in California found that this species had two generations and appearing a month and a half earlier, but concluded its development equally early in the fall as is characteristic of the southwest region. The grape leafhopper had, by practically all superficial workers been credited with a considerable number of generations. Slingerland, by careful and thorough work, reduced this to a possible two. Quayle, under the most favorable possible conditions for a continual production of generations, was unable to find any trace of mating or reproduction in the second brood adults. He did not, however, follow his first generations through and it may possibly be that the second generation was not a complete one even in that region.

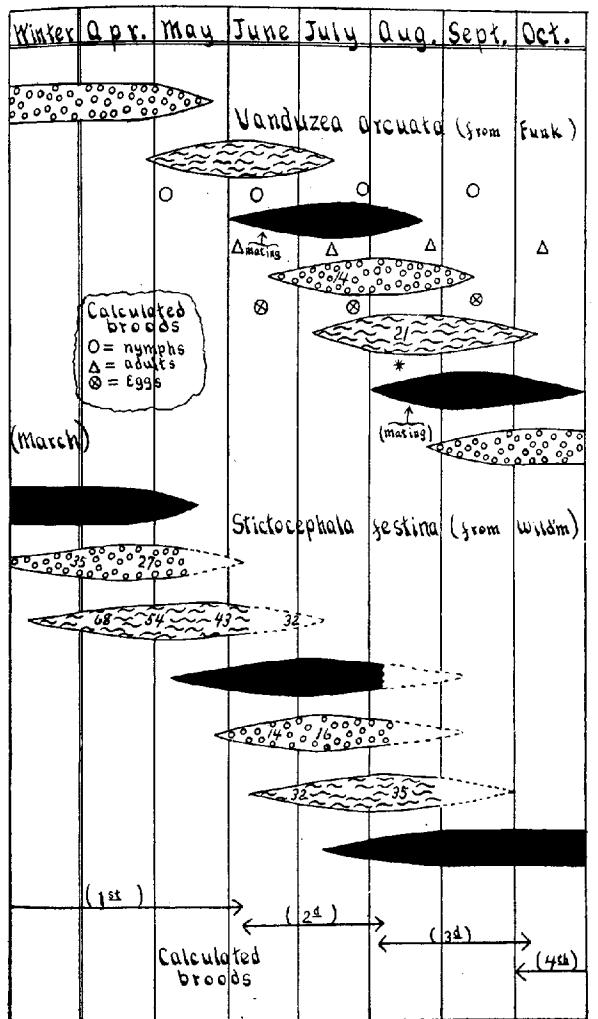
The writer has shown that in the single brooded beet leafhopper the nymphal period varies from April and May in Arizona to July and August in Idaho, and that there are all gradations in the intervening regions without changing the single brooded condition. This species is adapted to feeding on the plants of the beet family and the single generation appears in a region at the time when the food plant is making its most rapid growth.

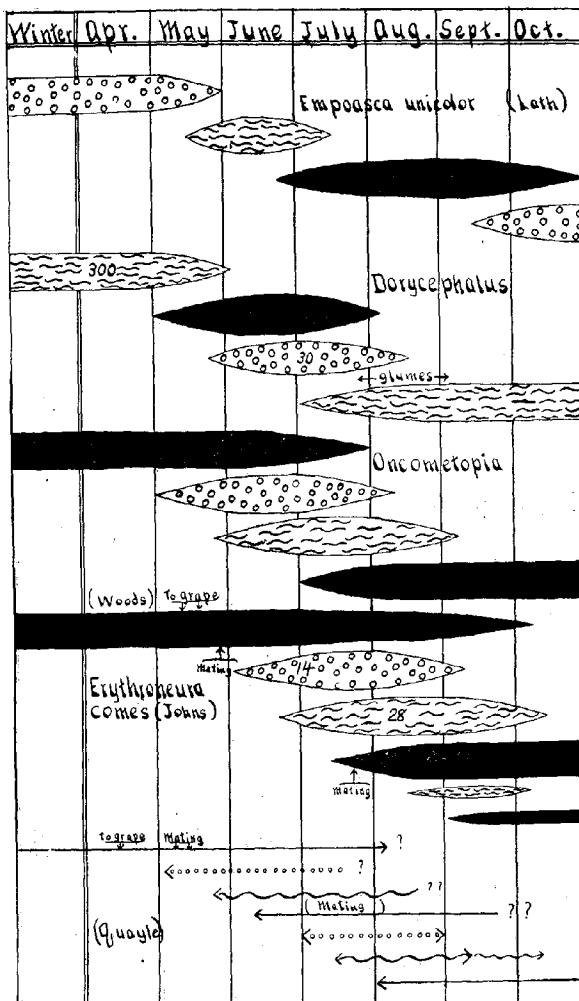
The problem of obtaining continuous cage records from generation to generation, with such delicate and active insects as the major portion of the leafhoppers have proved to be, is one of the greatest obstacles to accurate knowledge of this group and no doubt one of the fruitful causes of the mathematical propensity of some of the workers. There are, however, a number of ways of determining what is occurring in the field and in checking up incomplete cage records, even where there is an apparently continuous production of nymphs and adults. The most important single landmark of the season is the mating period. If mating is observed in abundance a new generation will soon follow. This is the time when flights occur, migration takes place, and at this time males often fly to lights in numbers. If on the other hand a great preponderance of females are found it will be the later stages of the egg deposition period. The males are always the first to mature and then there is a short period during which the sexes are equal while the last remnants of a brood of adults are always females. If males and females are abundant and no mating is taking place, superficial dissection of the female will at once show whether eggs are present. In cases of adult hibernation the fall generation does not mate and no eggs develop that season.

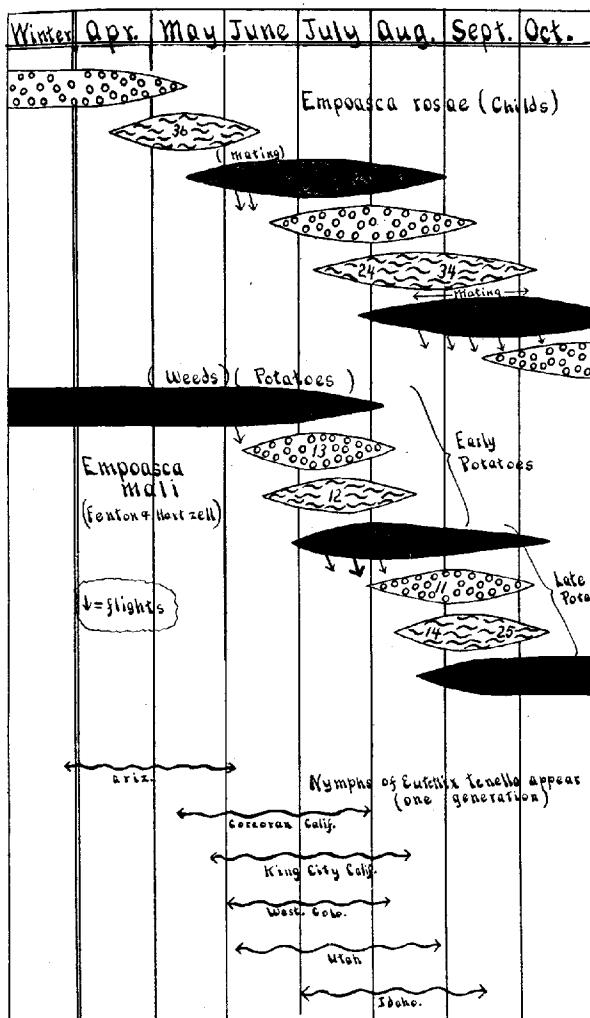
In the HETEROPTERA we find a very similar condition with respect to generations. All species have at least one generation a year while few if any have more than two. Adult hibernation is very common in this group, in fact, it is the rule in a large number of families and occurs in nearly all of them. Mating is very conspicuous and takes place through a considerable period, thus giving a guide to the generations. The eggs in a number of groups are deposited on the leaves and are easily observed.

The chinch bug which used to range from northern Wisconsin to Texas, had two annual generations and adult hibernation throughout. Its relative, the false chinch bug, appears to have a similar life cycle although a recent writer announces four generations. His four broods were mathematically calculated but he naively noted that it was very difficult to obtain nymphs during two of the periods while during the other two they were abundant.









4. THE LIFE CYCLE OF APHIDS AND COCCIDS.*

EDITH M. PATCH,
Maine Agricultural Experiment Station.

APHIDS.

To attempt to epitomize the life cycle of the aphid is like trying to draw an orderly sketch of Chaos. But after all, the confusion may be more seeming than real and certain rules, beset though they may be with exceptions, govern the life of even the aphid.

The gamogenetic egg is an outstanding argument for the conclusion that the aphid of the North is holding more closely to its prehistoric past than are those that spend their lives where the successive seasons of the year offer a constant source of food. For in the region of real winters there is no member of the family Aphididae (in its restricted sense) whose total life history has been worked out, that is known to pass its annual cycle without exhibiting a concluding generation comprising both sexes. The aphid, then, starts its life cycle like a typical insect—in the fertilized egg.

The overwintering egg is thus true to the traditions of the Hexapods, but with it ends all conventional observances, for between one such egg and the next in sequence there are crowded such phenomena as a succession of parthenogenetic viviparous generations; extreme examples of polymorphism; alternation of generations in a series where a duplication may not occur for seven or more generations; parallel series in which certain females give birth to true sexes without beaks while others of the same generation give rise to normal young which hibernate in the first instar without feeding; and a system of seasonal migration which is not surpassed by any other in the animal kingdom. That all these divergences from the ordinary life cycle for insects take place within the limits of the family Aphididae would seem remarkable indeed; but it is no less than appalling to realize that the total range of phenomena just indicated may be exhibited by a single species.

*These groups share with other Homoptera the general heterometabolic or "gradual" metamorphosis, but present a bewildering array of specializations and adaptations.

• Papers from the Maine Agricultural Experiment Station: Entomology No.106.

For the purpose of illustrating such a cycle, which will give a representation of the family in the complex estate which many of its members have attained, we might focus our attention on that common, widespread, and well known aphid, *Eriosoma lanigera*, with reference to the outline, Chart II.

I. APHIDIDÆ.

FORMS AND SEQUENCE OF GENERATIONS TYPICAL FOR MIGRATING APHIDS.*

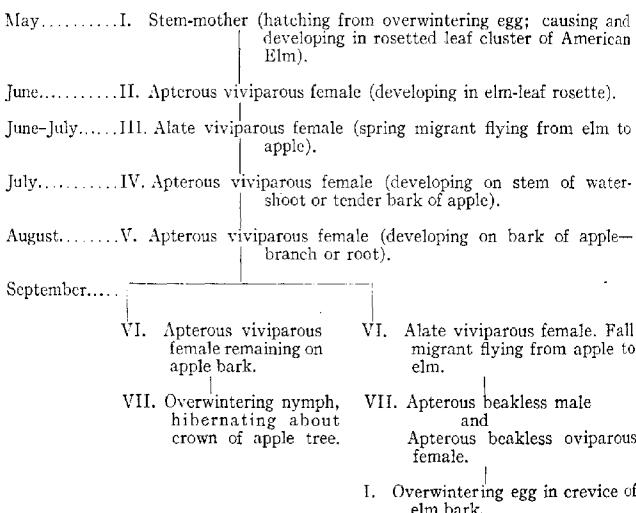
I. Fundatrix	(4)	apterous, parthenogenetic, viviparous female—hatching from the overwintering egg and living on primary host.
II. Spuriae apteræ	(1)	parthenogenetic, viviparous females—living on primary host.
III. Spuriae alatae	(1)	parthenogenetic, viviparous females—developing on primary host and migrating to secondary host.
IV. Spuriae apteræ	(2)	parthenogenetic, viviparous females—developing on secondary host.
V. Sexuparae alatae	(3)	parthenogenetic, viviparous females—developing on secondary host migrating to primary host.
VI. Sexuales		males (4) and oviparous (4) females.
I. Eggs	(4)	on primary host.
(1) The second and third generations, with certain species, may comprise both apterous and alate females; or there may be several generations of either the apterous or the alate females.		
(2) There may be two or more generations like IV which are usually counterparts of II.		
(3) The fall migrants may resemble III closely or they may differ markedly.		
(4) These appear but once in the annual cycle.		

* The terms applied to the different aphid forms are very numerous. A tabulation of these for uniform reference would be interesting and convenient but too detailed to be in keeping with this brief paper.

The beautifully elaborated relation of this insect to the nature of its environment, and more the way in which it controls and selects its environment, results in a life history the events of which are as thrilling as a tale of enchantment. The stem-mother touches the unfolding elm leaf with her wizard beak and the magic castle appears with its ample shelter. Its

living wells throb with the sap of growth from which the witch drinks and becomes the giant mother of two or three hundred sireless daughters born at the season when sap runs freely and growth is easy. These in turn give birth to unfathered daughters threatened with disaster. A thousand hungry beaks drain the castle wells of their sap. The floors run with honey dew, and

II. LIFE CYCLE OF *Eriosoma lanigera*. WOOLLY APHID OF THE APPLE.
Seven Generations.



(This outline is in accordance with the Maine schedule, in which connectioⁿ it might be stated that the overwintering nymphs are, for the most part, a luckless lot. *Proctiphilus tessellata*, however, which exhibits similar parallel cycles brings through the hibernating nymphs with much success).

mold appears. The murderous gangs of capsid, beetle and syrphid enter. And lo, the aphid but unfurls her migrant wings and seeks the juicy stem of an apple, clean and unknown to the enemies of her kind. Her daughters, lacking the leafy shelter of the elm, throw between them and the sun a waxy fluff and thrive. But her great-granddaughters find the bark of the

apple less generous for their needs, and their ancient enemies have smelled their blood and come to slaughter under the roof of wax. And then the migrant, true to the instincts of the clan in the hour of need, quietly escapes and bears the torch of life home to the elm. This voyage of the fall migrant seems inexplicable. It is neither her hunger nor that of her unborn brood that urges her forth for neither she nor her dwarfed, beakless progeny feed on the elm. It is not a quest for a mate, for she, like her maternal ancestors for five generations, gives parthenogenetic birth to her young. But, whatever the cause, once and once only in seven generations the fall migration takes

III. HORMAPHIDINI. LIFE CYCLE OF *Hormaphis hamamelidis*.

(Three generations).

- I. Fundatrix.....apterous viviparous female; hatching from overwintering egg; causing and developing within the witch hazel gall; reproducing by parthenogenesis.
- II. Sexuparæ alatae.....Alate viviparous females; developing within the witch hazel gall; dispersing to witch hazel leaves; reproducing by parthenogenesis.
- III. SEXUALES.....dwarf, apterous male and oviparous female; both with beaks developing on witch hazel leaves; female laying several fertilized eggs.
- I. Eggs.....overwintering on witch hazel.

(For the vicinity of New York, adapted in part from T. H. Morgan and A. F. Shull)

place from secondary to primary host, as once and once only in seven generations the reverse migration of the spring occurs.

Any one such life cycle as that just indicated, though representative, must be specific rather than comprehensive.

An inter-food-plant migration would seem to have become typical of the Aphididae, for it is met in ten* or more widely distributed tribes; although in many instances the migration is restricted to fresh plants of the same species, a modification that obscures its significance.

That the environment is influential in the production of the winged forms, thus giving the mechanism for migration, is

*Aphidini, Myzini, Macrosiphini, Anoeciini, Mindarini, Schizoneurini, Pro-ciphilini, Pemphigini, Hormaphidini, Pterocommini.

IV. CHERMISINA.* (LIFE CYCLE TYPICAL FOR CHERMES).

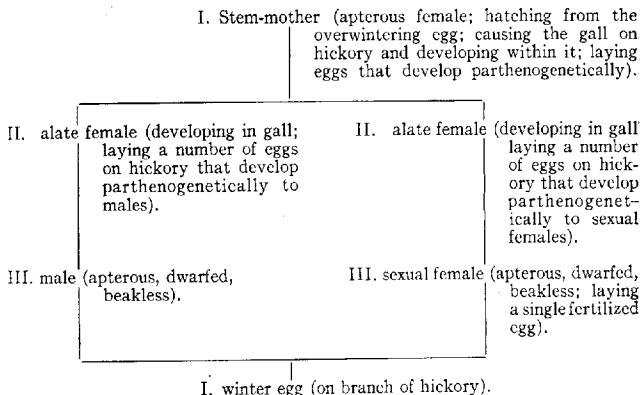
	Primary Host, Picea	Intermediate Host, Larix (or Pinus or Abies)
1st Year	I. Fundatrices (hibernate—cause gall—wingless, all ♀) II. Alatae (larvae inhabit gall— Non adults winged, all ♀ migrantes Migrantes	
2nd Year	I. Fundatrices (as before)	III. Colonici (hibernate—cause no gall—wingless, all ♀)
	V. Sexuales (wingless— cause no gall) II. Alate (as before) Non-migrantes Migrantes	IV. Sexuparæ (adults winged) Exsules (adults wingless) Exsules
	I. Fundatrices	I. Fundatrices
		?

* No longer included with the family Aphididae in its restricted sense.

(Adapted from E. R. Burdon, Proceedings of the Cambridge Philosophical Society, Vol. XIII, Pt. 1).

indicated by the circumstance that the best defined examples of migration are exhibited by gregarious species and is correlated with the exhaustion by the aphids of the infested food-plant in the spring and with either that or a normal ripening of the food-plant in the fall. The evidence of Shinji, based upon food tests under chemical control appear to be of especial significance in this respect.

V. PHYLLOXERINÆ.* LIFE CYCLE TYPICAL FOR THE PHYLLOXERANS.



* No longer included with the Family Aphididæ in its restricted sense.

Although the testimony of aphids in the North emphasizes the annual occurrence of the fertilized egg, the parthenogenetic reproduction, which is characteristic for all but a single annual generation, may in many species be indefinitely continued in a warm climate or in hot house conditions (as witness Ewing's 87 generations with *Aphis avenæ*). Whether temperature is the direct control in such cases may be doubted for we have many species producing both alate and apterous forms throughout the summer; and it may be that the continual vegetable growth made possible by the warm climate is the direct encouragement to parthenogenetic viviparous reproduction. This supposition is accentuated by the fact that even in tropical climates experiencing a wet and a dry season gamogenetic eggs are produced to

tide over the period of famine; and in the North some non-migrating species produce the sexes in August, July or even June on exhausted vegetation.

The parthenogenetic type of reproduction, correlated, as it were, with the abbreviated time required for the development of the individual, makes possible the enormous increase of the aphid colony and at the same time minimizes the numerical importance of the gamogenetic egg. We find, then, one of the very striking differences between these and other insects, in the fact that the oviparous female of the aphid never deposits more than a few eggs and in certain tribes one egg only of this character is produced. As if to further emphasize the significance of parthenogenesis for the aphid, certain species (as *Eriosoma lanigera* and *Prociphilus tessellata*) even when dwelling in the North, attempt to provide for a continuation of the apterous, viviparous, parthenogenetic part of their cycle by producing annually nymphs to hibernate about the base of the secondary host at the same time that the migrants are producing the sex forms on the primary host.*

COCCIDS.

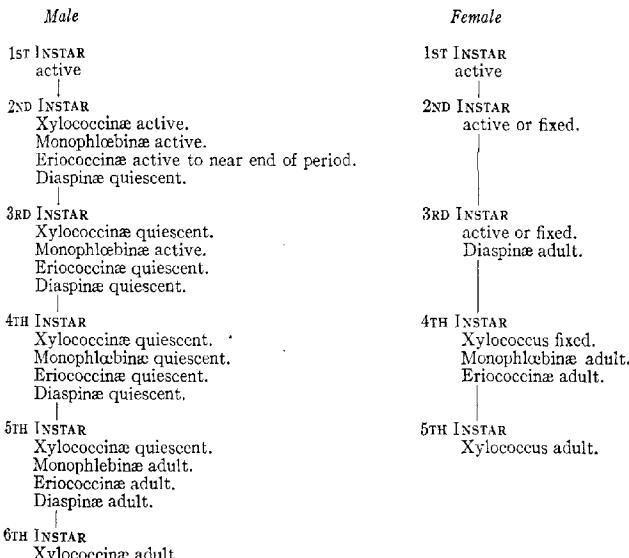
The eccentricities of the coccids are concerned with the specialization of their structural characters, and the modified metamorphosis of both sexes rather than with any striking range of habit or peculiarity in sequence of generations; since their typical life cycle comprises between one fertilized egg stage and the next but a single generation composed of both sexes. The extreme possibilities of coccid metamorphosis are illustrated by those species in which the females, at their first molt, lose, for good and all, eyes, antennae and legs, exhibiting in this atrophy of those organs of orientation and locomotion, a trans-

*In the preparation of this paper repeated attempts have been made to broach the aphid cycle in general terms, a process that would force us to build upon a hypothetical type reminiscent of a primitive condition when each generation was composed of males and females, both alate, and when propagation was solely by means of the gamogenetic egg as is typical for the class Insecta; but not only is such a lost type hypothetical for the aphids, but the processes of divergence have been so marvelously complicated, as concerns structure, habit, and sequence and combination of generations, that the hope of correlating the different groups on any graphic basis has been abandoned; and representative glimpses are all that the accompanying outlines offer.

Appreciative thanks are due Dr. A. C. Baker, Dr. O. W. Oestlund and Dr. Herbert Osborn for reading the paper critically and for certain suggestions that have been incorporated.

formation which has to do with the loss of such organs as characterized them as insects in the first instar, rather than in the acquisition and development of the structures of an adult hexapod. This metamorphosis by reduction, associated with the complete absence of wing development in the female is correlated with the sedentary habit of this family and is in line

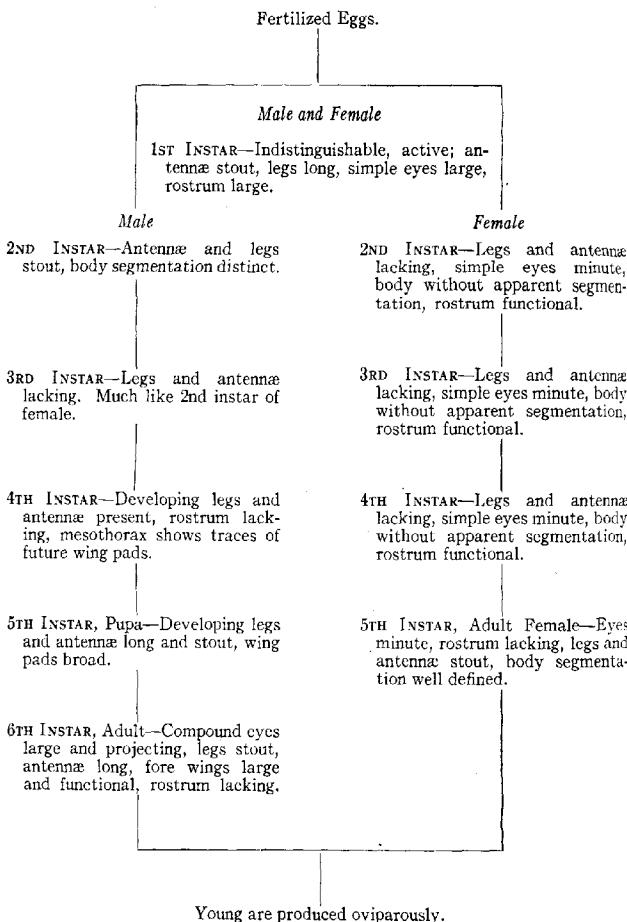
VI. COCCIDÆ. GENERALIZED OUTLINE.*



* This outline is given by courtesy of Dr. A. D. MacGillivray, to whom thanks are also due for a critical reading of the Coccid part of the present paper and for certain suggestions that have been incorporated.

with the atrophy of class structures in parasitic animals. But the suppression of generalized characters does not inhibit the appearance of special structures of a high degree of development, as is beautifully illustrated by the wax glands, marvelous in form and variety, to be found in the coccids; a concentration of structural effort directed toward the secretion of a waxy protection for these sedentary creatures and their eggs.

VII. COCCIDÆ. LIFE CYCLE OF *Xylococcus betulae*.



(Adapted from Hubbard and Pergande.)

The metamorphosis of the male coccid falls in line with that of the female for the first, and in many respects for the second instar.

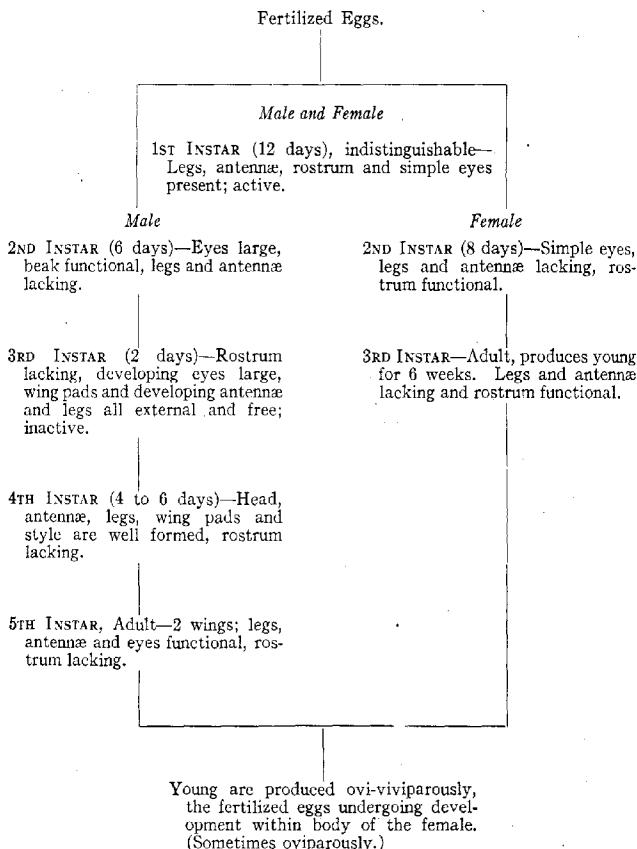
Then, as though the somatic memory of Hemipteron inheritance reclaims its own, the insect reverts to the methods of the order to which it belongs and develops antennæ, legs and wings by the external gradual process proper to the Rhynchota. In the confusion, however, between the generalized Hemipteron transformation by gradual external development of adult characters, and the specialized tendency of the parasitic coccid toward atrophy of these same characters, the male, attempting both, accomplishes neither in typical shape; but strikes a happy medium all his own by passing through his latter nymphal instars beakless and quiescent, and emerging a queer atom of an insect in possession of remarkable eyes, well developed legs and antennæ, and usually functional wings (albeit there is little left of the hind pair but the costal hooks), but lacking curiously enough the only emblem of Homopteron relationship which his wingless, eyeless,* legless,* antennaless*, mate can boast—the beak*.

The biological urge for overproduction is chiefly provided for, among the coccids, by the great number of eggs deposited rather than by a conspicuous shortening of the life term of the generation. Coccid eggs are typically fertilized though there are many instances of parthenogenetic eggs recorded. Parthenogenesis in the coccids, however, does not seem to function toward a greater number of generations per season as with the aphids but is merely an alternative of certain species. This is also the case with the ovo-viviparous reproduction of those species where the egg undergoes complete development and hatches within the body of the living female; a process which does not carry the significance of the viviparous reproduction of aphids.

Except for those species for which apterous and alate males both occur, polymorphism is not exhibited by the coccids, nor do they have an alternation of generations—one being like another in form and habit. Perhaps nowhere else among the insects, however, do we find a more excessive difference in the two sexes than in the extraordinary dimorphism of the coccids.

*This, of course, can not be said of the whole family. The female, *Xylococcus betulae*, for instance, possesses eyes, legs and antennæ and lacks the beak!

VIII. LIFE CYCLE OF *Aspidiota perniciosus*.



(Adapted from Pergande, 1895.)

The sedentary habits of the female scales leave the natural dispersal of these insects to the first instar larvæ so that, except for accidental carriers, the spread is characterized by its thoroughness rather than by its breadth.

The most congenial conditions for the coccids are found in warm climates, and there are comparatively but few species whose life cycles are attuned to regions having severe winters.

5. THE LIFE CYCLE OF THE LEPIDOPTERA.

S. B. FRACKER,
Madison, Wis.

Coming at the point in this program between discussions of heterometabolous and holometabolous development, it seems necessary for us to diverge a few moments from the subject as printed, to consider the biological significance of complete metamorphosis.

The structural basis for the distinction between these two types of development has been repeatedly described. Studies histological, morphological, and physiological, have been made on the ontogeny of the different parts of the insect body, in ametabola, heterometabola, and holometabola. Uniformity has been discovered in wing development, cell structure, and body sclerites within each of these groups until we may say that the basis for the three great subclasses of insects rests on a solid foundation in morphology.

The biological significance of these groups, on the other hand, has usually been overlooked. The environmental problems which evolution is called upon to solve, if we may be permitted to express the situation in this way, become immensely complicated as the number of different forms taken on by a single individual increases.

Speaking biologically then, insects without metamorphosis exist in, and are thus adapted to, a single environment, both the form and the surroundings remaining the same throughout the life of the individual. With the arrival of wings, an increase in the number of activities causes an enlargement of horizon and introduces some degree of variety in the character of the

surroundings. Typically, heterometabola, except when aquatic, retain the same environment throughout life and the adults face practically the same ecological conditions as do the immature, wings simply increasing the chances of survival.

Insects with complete metamorphosis all differ from those with incomplete, in one respect: to each individual three environmental problems are presented. The larva must find an adequate food supply, the pupa protection against enemies and hostile physical conditions, and the adult opportunity and means for reproduction. The abundance of the available food, which includes every kind of organic matter, elaborated in any way by any vegetable or animal organism, reduces the complexity of the situation. Rapidity of locomotion, however, one of the most effective means of escaping adverse conditions, has been uniformly reduced or lost in holometabolous insects. For the latter, therefore, the problem of utilizing the food supply is one of protection against enemies and weather during the period of growth.

If we now turn our attention to the position of the Lepidoptera among other holometabola we find that the four major orders have solved this problem of protection in four different ways. The Coleoptera use the combative method of fighting the struggle for existence. Clad in armor in both larval and adult stages they exist on the hardest wood, prey on the most agile insects, or burrow within the soil. The Diptera, on the other hand, have adopted the path of least resistance. While the armed beetle larva hides in caves and burrows, the dipterous maggot is concealed deep in rotting vegetation, in the stomachs of mammals, or the body juices of other insects. Even the predacious Syrphid larvæ attack only the softest, most helpless of all insects, the plant lice.

Hymenopterous larvæ, excepting the Tenthredinoidea, have, if anything, gone farther. Many still "rustle for themselves" but in the more specialized predatory families even the host insects must be paralyzed by the parents before the larvæ can successfully attack them. Finally the last step is reached among the bees and ants where the young must be fed, warmed and cared for day by day, so utterly helpless that they can not even be furnished with an adequate supply of food and left to consume it alone.

Of all the major orders, in only one, the Lepidoptera, have the larvæ attempted to meet the conditions of life as it exists and, with minimum protection, succeeded solely through their immense vitality.

If the uniformity within each dominant order is remarkable, the variety is no less so. The differences between the nearly fifteen thousand species of Coleoptera in the United States are primarily variations in essential chitinized structures. Number and position of legs true and false, number of claws, shape and arrangement of mouthparts, head skeleton, cerci, and chitinized plates are all evident. In the Diptera structural differences are equally numerous; the soft parts such as body shape, and the respiratory system are also various. Dipterous larvæ depart farther from typical arthropod structures than other orders.

In the Hymenoptera structural divergences (once more excepting Tenthredinoidea) almost disappear and variation in social organization and methods of securing food take their place.

Again the Lepidoptera are unique. With a fundamental structure so constant that logical classification long appeared to be baffling, superficial differences in the larvæ are extremely numerous. One finds remarkable uniformity in all the principal features of anatomy. The same number and position of thoracic legs and prolegs, the latter nearly always with chitinized hooks, the same form of head, the same kind of mouthparts, the same number of spiracles and segments. Exceptions, except among the few leafminers, are trifling.

In superficial characters the reverse condition, variety, is just as marked. Using one fundamental setal pattern, the most diverse arrangements are presented. A sensitive area in one family develops a single seta, in another, a tuft on a wart, in another, a group of soft hairs on a flat plate, and in still another, a bunch of poisonous spines. If we examine the arrangement of the hooks on the prolegs we will note variations equally significant.

FOOD SUPPLY

Table I shows the remarkable uniformity in source of food supply in the Lepidoptera. The members differ from other orders in being confined almost entirely to chlorophyll-bearing plants. The exceptions are entirely among the more primitive

microlepidoptera. In the families in which the mode of life has become static, the species are limited not only to the kind of plant, but are, except in a few Noctuidæ, confined almost wholly to leaves of terrestrial flowering species.

TABLE I. FOOD SUPPLY.

ORDER, FAMILY, OR SUPER-FAMILY	PLANT MATERIAL						ANIMAL MATERIAL			
	Living Terrestrial Flowering Plants			Aquatic Plants	Dead Plant Material	Fungi	Living	Dead	Dried	De- cayed
	External Leaf Feeders		Borers	External Leaf Miners	Borers, Leaf-rollers, or Webbers	Dried Fruit, Nuts and Vegetables	(Except occasionally Fungous Spores)	Parasites or Predators	On Invertebrates	On Vertebrates
	External Leaf Feeders	External Leaf Miners	Borers	External Leaf Miners	Borers, Leaf-rollers, or Webbers	Dried Fruit, Nuts and Vegetables	(Except occasionally Fungous Spores)	Parasites or Predators	On Invertebrates	On Vertebrates
NEUROPTERA.										
MECOPTERA.										
TRICHOPTERA.										
LEPIDOPTERA.	X	X	X	X	X	X				
Tineoidea...	X	X				X		X		
Tortricidae...	X									X
Aegeridae...			X							
Cossidae...			X							
Psychidae...	X									
Gelechioidea...	X	X	X	X	X	X				
Pyralidoidea...	X	X	X	X	X	X				
Zygaenoidea...	X							X		X
Geometridae...	X									
Lasiocampidae...	X									
Liparidae...	X									
Notodontidae...	X									
Noctuidae...	X	X	X	X	X	X				
Arctiidae...	X									
Saturnioidea...	X									
Sphingidae...	X									
Hesperioida...	X									
Lycenoidea...	X									
Nymphaloidea...	X									
Pieridae...	X									
Papilionoidea...	X									

Note—Parentheses indicate rare or unusual sources of food for the group named.

Returning to our original figure of speech, nature has taken a fundamental structure and a relatively constant environment and through superficial modifications has developed a great dominant order. She has exposed the members to every form of attack from parasites and enemies. She has made them both conspicuous and slow, with only moderate fecundity. But by providing them with the most universal and abundant source of food she has so developed their vitality that they have become

one of the four largest groups of ordinal rank in the animal kingdom.

The few exceptions to the phytophagous habit include such very rare parasites as the Xylorictidæ, and a few predators such as one or two pyralids living on scale insects. Possibly the clothes-moths and the wax moths, living on animal products, might also be called carnivorous. None are parasites on living vertebrates.

TABLE II. MEANS OF PROTECTION.

ORDER, FAMILY, OR SUPER-FAMILY	STRUCTURAL	EXTERNAL										ARTIFICIAL	
		NATURAL					ARTIFICIAL						
		Hairy	Non-Poisonous Spines	Poisonous Spines	versible Glands (Repugnatorial?)	Sting or Bite	Defensive Coloration	Conspicuous, No Protection?	Leaf Miners	Leaf Rollers	Stem Borers	In Fruit or Nuts	
NEUROPTERA													
MECOPTERA													
TRICHOPTERA													
LEPIDOPTERA	X	X	X	X	X	X	X	X	X	X	X	X	X
Tineoidea													
Tortricidae													
Aegeridae													
Cossidae													
Psychidae													
Gelechioidae													
Pyralidoidea	X			X									
Zygaenoidea	X			X									
Geometridae							X	X					
Lasiocampidae	X						X	X					
Liparidae	X	X	X	X									X
Notodontidae	X	X	X	X	X	X							
Noctuidae				X	X								
Arctiidae	X									X	X	X	
Saturnioidea		X	X				X	X					
Sphingidae							X	X					
Hesperioidae							X			X			
Lycaenoidae	X	X	X										
Nymphalidae													
Pteridae				X		X	X						
Papilionoidea													

FORMS OF PROTECTION.

In Table II the possible forms of protection against adverse conditions are shown divided into "structural" and "external" classes; the former depend on anatomical adaptation, the latter on habit and mode of life. Here as in Table II, the division

between microlepidoptera and the macros appears plainly and has greater biological significance than the division into moths and butterflies.

The members of the first half of the order, the microlepidoptera, show the anomalous condition of greater variety of habitat and food supply, associated with a most extraordinary uniformity in structure (excepting in leaf miners). Nearly all the exceptions to rules occur in this group. In the more specialized suborder on the other hand, one finds remarkable uniformity in habits and food but a great variety of superficial appearance.

The two most common forms of protection in Lepidopterous larvæ are (a) the development of tufts of setæ and (b) the construction of a nest or case. Silk glands are of universal occurrence but are used in many different ways with different results. The effective value of tufted setæ against birds, parasites, and predators is well known.

LIFE CYCLE.

Leaving these general considerations of lepidopterous development, a brief statement on the length of the life cycle should be included in a paper on this subject. Typically the life of a lepidopterous insect consists of (a) an egg stage, the egg simple in structure and seldom concealed; (b) the larval period, of five to seven instars; (c) the pupal condition, protected by a cocoon, or, in form, a chrysalis; and (d) the adult relatively constant in structure, and various in appearance like the larva.

The number of broods is limited, Table III showing the conditions in economic species in the northern States. One or two broods a year are the rule, longer or shorter life cycles being exceptional. The writer is familiar with no cycles longer than one year outside the family Cossidæ.

More than three annual broods occur only in the southern states or under conditions where breeding throughout the year is possible. Seven broods in one year in a species living in grain (Angoumois grain moth) seems to be the maximum authentic record.

The winter is usually spent as a larva, often followed immediately by the pupa in the spring without resumption of feeding. This is true in both one and two brooded species. In some single-brooded forms the egg stage is the hibernating condition

while in a few species the pupa or adult manages to survive the winter.

The fundamental basis of lepidopterous development appears to be the combination of a universal food supply with a remarkable uniformity in structure in all stages. Thousands of species

TABLE III. BROODS AND HIBERNATION.

FAMILY OR SUPER-FAMILY	NO. OF SPP. REC.	BROODS					HIBERNATION				
		½	1	2	3	4-6	E	L	P	P-A	A
Tineoidea.....	6		4	2		(2)		3	2		
Tortricidae.....	13		3	8	2-(2)		3	5	3		
Aegeriidae.....	4		4	(1)				4			
Cossidae.....	2	2						2			
Psychidae.....	1		1				1				
Gelechioidae.....	2							1	3		
Pyralidoidea.....	17		4	8	3	(8)		8			
Zygaenoidea.....	1		1					1			
Geometridae.....	7		6	1			4	1	1		
Lasiocampidae.....	2		2				2				
Liparidae.....	5		5				4	1			
Notodontidae.....	3		3	(1)			1	2			
Noctuidae.....	18		6	10	1	(4)	1	4	7	2	1
Arctiidae.....	5		4	1			1	5			
Saturnoidea.....	3		3					2			
Springidae.....	6		6	(2)				6			
Hesperioidae.....	1					(1)					
Lycaenoidea.....				1							1
Nymphaloidea.....	1										
Pieridae.....	3			2	(3)						
Papilionidae.....	1			1							
TOTAL (Nearctic).....	101	2	51	33	9		16	36	27	2	2
(Subtropical or protected)				(4)	(3)	(19)					

NOTE—Parentheses indicate the life history in the southern states or under indoor or stored-product conditions.

E—Egg; L—Larva; P—Pupa; P-A—Emergence during hibernation reported; A—Adult.

have evolved, all different in appearance, armature, and superficial characters, but remarkably alike in functional external organs of ingestion and locomotion. The "butterfly" is the proverbial example of superficiality but the lepidopterous larva and adult have such a healthy, tremendously vital basis on which to build that they must be considered in every sense successfully adapted to their world.

6. THE LIFE CYCLE OF THE COLEOPTERA (Including the Strepsiptera).

ROYAL N. CHAPMAN, University of Minnesota.

The magnitude of variations in the life cycle and form changes which are met with when the Coleoptera and the Strepsiptera are considered as a group are hardly exceeded by any other group of insects. When we remember that there are now considered to be more than one hundred families of Coleoptera containing, in all, over one hundred and fifty thousand species, it is not surprising that there is a great amount of variation.

Some of the standard works on the Coleoptera might lead one to believe that beetles have no larval or pupal stages, for they are not mentioned. When Buetenmuller published his catalogue of the described transformations in 1891, the eggs had been described for 52 species, the larvæ for 368, and the pupæ for 96 species in North America. While a considerable amount of progress has been made since that time it has been only during recent years that attempts have been made to correlate the knowledge of the transformations of even the smaller groups.

It is difficult to obtain accurate information with regard to the various life cycles, especially with regard to the conditions which cause variations in the duration of the various stages. The data on which this paper is based have been taken in part from statements in literature which seem to be dependable, and in part from original experimental evidence.

The type forms of the various stages of the life cycle are subject to great variation throughout the group. The majority of the eggs are laid singly and unprotected, but the hydrophylid eggs are in covrcd cases and some of the Carabidae deposit their eggs in cases constructed of mud. The egg stage is eliminated among at least some of the Strepsiptera which are viviparous.

The commonest larval form is campodiform or eruciform, being elongate and possessing thoracic legs, but all types of larvæ are represented. The generalized carabid larvæ are

typically campodiform, some of the Tenebrionidæ may be taken for the eruciform, while certain of the Buprestidæ, Cerambycidæ, Ipidæ and others represent the apodiform type.

The metamorphosis is complete, but there are cases of hypermetamorphosis. Among the Meloidæ we have this specialized type of development which illustrates, in a single species, all three types of larvæ, the campodiform, the eruciform (perhaps more scarabeoid) and the apodiform. There are other changes of form from one instar to another in the case of *Taphrocerus* (Buprestidæ) which hatches with the structure of a typical wood borer, but which appears later with the structure of a typical leaf miner. Some of the Bruchidæ have small functional thoracic legs in the first instar, but after they enter the nutrient substance in which the remainder of their life is to be spent, they become apodiform.

The pupæ are usually soft and protected from evaporation by a cell formed from materials of the environment cemented together by a secretion. However, some of the leaf miners which pupate in the leaves where the thin epidermis gives them little protection (*Taphrocerus*, Buprestidæ) are covered with a coat of chitin.

Most adult beetles are similar in general form, but the Platypyllidæ are parasitic upon beavers and resemble other parasites which live upon vertebrate hosts. Indeed they were first described as Mallophaga. Specialization has led to degeneration in the case of the rhipiphorid parasite of the cockroach, the female of which is larviform. Among the Strepsiptera there are cases which have gone much farther and the female is a sack-like organism without means of locomotion which remains attached to its host throughout its life and from which the young emerge as larvæ.

The number of broods, the length of life and the number of molts are of the greatest significance in this consideration. These are interdependent and inseparable. There is no great uniformity in these respects when the group is considered as a whole nor is there always constancy even within a single species. Changes in certain environmental factors may alter the number of broods, change the length of life and the number of molts. But it should not be concluded that a change in a certain factor will cause a change in all species, or that some species can be changed at all. Nor are we justified in concluding, *a priori*,

that even the inherent tendencies toward periodicity may not be altered. In general those forms which are found in more or less uniform environmental conditions respond most readily to changes of the environment. Examples of this may be found among the beetles which live in stored food products. On the other hand, the beetles which feel the effects of the periodic changes of the season, having their food available for a limited period of each year, often have developed a periodicity with regard to their life phenomena.

Tribolium confusum has its egg stage shortened from ten to five days by a rise of from 24° to 34°, and it will develop one generation after the other throughout the year. On the other hand, the life cycle may be prolonged by a reduction of the amount of moisture and also by a limitation of the quantity or quality of the food. Thus the length of life and the number of broods may be altered by changing any one or all of these three factors. A larva now under observation has had its life prolonged from thirty to ninety days due to food conditions, and during this time it has molted twelve times rather than the normal six times.

So far as is known, all beetles have their lives shortened by an increase of temperature, over that which they normally experience. But some of them will not produce more broods in a year under high temperature than under low. The cotton boll weevil, a native of the south, has been reported to have as many broods a year as time, temperature, and humidity will allow, but the potato beetle always has two broods a year. Those forms which are not subject to an inherent periodicity have more broods in the south than in the north, but those with a fixed periodicity cannot be so changed. Shelford reports that a certain cicindelid has the last larval instar prolonged to extend over the period of hibernation in Canada, while the same species has a shorter larval life in the vicinity of Chicago.

The Buprestidæ as a family hibernate in the larval stage, but *Taphrocerus* which mines in the leaves of the floodplain bullrush as a larva, emerges and hibernates in the adult stage. In this case the larval life is confined to about six weeks in the early part of the summer and the adult beetles emerge and feed about on the leaves, but no eggs are deposited until the following spring. On the other hand, the larvæ of *Agrilus bilineatus*, a wood-boring buprestid, may mature in August and form their

pupal cells, in which they will remain as larvæ until the following spring, even though the temperature rises during September and there is ample time for them to transform and emerge as adult beetles. However, there would not be time for the eggs to be deposited and hatched and for the larvæ of the next generation to penetrate the bark of the tree before winter.

Among some of the Staphylinidæ which are reported as being symbiotic with ants, the larval life is said to be only fourteen days. On the other hand there are cases reported in which certain of the Cerambycidæ have been known to live as larvæ for years in dry wood.

If a statement were to be made with regard to the usual length of the egg stage of the Coleoptera as a whole, it would probably be to the effect that the egg stage is normally ten days in length. The Staphylinidæ already referred to as being symbiotic with ants, have an egg stage which is said to be of only two days duration. Still others of this same family have no egg stage at all. Several species of the Chrysomelidæ and the Strepsiptera are also viviparous.

The adult life is no more constant throughout the group than the other stages are. The adult life of many beetles coincides roughly with the growing season, although some of the Carabidæ have been observed to live for more than a year. Adults of the genus *Tribolium* have been kept for more than a year at room temperature and oviposition continued throughout this period. The males of some of the Strepsiptera are reported as living but fifteen or twenty minutes of extremely active life, while the females, in the absence of the egg stage, must live a more prolonged life in order that the young may develop within them.

The larvæ molt their skins in a more or less periodic way. Five or six instars may be considered as common, but among some of the Buprestidæ and others the number of molts may be increased when the larval life is prolonged as a result of unfavorable environmental conditions. One of the Tenebrionidæ has already been referred to as having had its life prolonged to three times the normal period during which time it has molted twice the normal number of times.

To turn to the consideration of the significance of these facts in relation to the environment it is necessary to avoid being lost in a vast amount of detailed information. In this

limited space it is possible to make only a few generalizations. A precaution may well be taken with regard to the use of the word "adaptation." In the minds of some of the modern biologists it is not orthodox to even mention this word. Therefore this word will not be used, but attention is called to the fact that the insects of this vast group are fitted into the environment wherever they will fit, with the result that certain type forms, together with certain biological characteristics, are to be found in the different types of environment.

There is a considerable group of aquatic beetles. Some of the larvæ crawl about over the submerged vegetation and resemble some of the neuropteroid larvæ of the same habitat as much as they do other closely related Coleoptera. In the swift water of a lotic environment the limpet-like larva of *Sphenus* is to be found.

A large group of beetles typified by the Carabidæ is found on the ground and under its cover of debris. The campodiform type of these larvæ has already been referred to and it is to be noted that this same type form is to be found among all surface feeding larvæ whether they feed upon the ground as the Carabidæ do or whether they are slightly modified for feeding upon the surface of plants as the Chrysomelidæ and Coccinellidæ do. These type forms, however, are characteristic of the families only in so far as the species retain the typical habits of the families. The family Chrysomelidæ has certain members which feed upon aquatic plants and these species have departed from the family type and have taken on various specializations leading to a virtual apodiform condition in some species.

Another great group of beetles passes the larval life within the nutrient medium. Some of these make their way through a hard substance with a great deal of effort and are typically apodiform. They are highly specialized for this mode of life and are helpless upon an exposed surface. Others which are normally found in softer substances may have well developed thoracic legs, as in cases where it is necessary for the larvæ to pass through a large amount of substance in order to accumulate enough nutrient material for maintenance and growth. Still others which live in a soft medium of high nutrient value may have limited means of locomotion and the entire larval life may be spent in a very limited space.

The more complicated life cycles have the most extreme changes of form connected with them, such as have been referred to in connection with the form changes of the larvæ. The Meloidæ are the best examples of this specialization, including such examples as *Epicauta*, the larva of which is at first camponiform and free living, but after it has located the egg pod of one of the Orthoptera, it enters into an arcuate larva with greatly reduced thoracic legs. Thus we have in a single life cycle a combination of the free living and restricted habits of life and they are accompanied by the typical larval forms which are to be correlated with them.

The impress of climate on the life cycle of the beetle is unmistakable. However, the effect of temperature upon the length of the various stages has already been referred to in connection with the length of life cycle and will not be discussed further.

Food is a factor which, like climatic conditions, may alter the length of the cycle as a whole or certain stages of it. This factor has been greatly neglected and a better understanding of it will undoubtedly be a great aid in bringing order out of the confusing detail which is to be met with in studying the biology of the Coleoptera.

The herbivorous beetles which are dependent upon growing plant tissue for their food may be said to have the factors of food and climatic conditions more or less merged into one. Conditions which favor the growth of plants favor the food supply, and thus control the growth and development of the beetles.

Beetles which live within their nutrient medium may be in the leaves of plants, in the fruiting bodies, or they may be in the supporting structures such as wood. These forms lend themselves to experimentation, for it is possible to correlate their rate of growth with the nutrient value of the material in which they live. The wood boring forms are notoriously long lived and the leafminers are usually short lived. Here with conditions of temperature and humidity constant it is possible to prolong or shorten the life cycle by controlling the nutrient value of the food.

The relatively simple condition just cited merges into a more complicated condition met with in the forms which are termed scavengers. While these forms appear to be subsisting upon

dead plant and animal matter, this material is teeming with life. The basic processes of ammonification, nitrogen fixation, and the synthesis of proteins are being carried on by these micro-organisms and the beetle which feeds upon this decaying matter profits by their activity. It has been shown, in the case of some insects, that under certain conditions the rate of growth is in direct proportion to the number of micro organisms in the food.

One has but to review the food lists of the beetles to note in how many cases they are known to feed upon fungi or upon substances which may well contain micro organisms. When this subject has been investigated further we may come to a newer and more rational understanding of the life cycle of the Coleoptera.

7. THE LIFE CYCLE OF THE DIPTERA.

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In attempting a summary such as this, one is almost dismayed by the great gaps in our knowledge of even the commonest species. Doubtless many of the gaps in what follows could be filled by a more careful scrutiny of the literature; many more, I am sure, could be filled from unpublished records and observations of the members of this Society; but when all this is recorded we shall find that very much more investigation must be performed before we can so much as give a comprehensive statement for all the species of a single family or for a single species of each family.

I do not believe that the order Diptera is surpassed, either within or without the class Insecta, for variety of habits and complexity of bionomics; and it seems to me an impossible task to present in a brief paper anything like a satisfactory picture of the life-cycle of the flies.

Not only is data wanting for more than a fraction of a per cent of the species; but, moreover, in the families where our knowledge is more complete, the most impressive thing is that *there is no agreement or uniformity of habit*. Where uniformity appears in my statements it is possibly because we know only a few of the many species in that group.

The Diptera all belong to the group variously known as Endopterygota or Holometabola or insects with a complete metamorphosis. Egg, larva, pupa and adult are very distinct from each other and usually well separated both structurally and ecologically. In fact, I have not been able to think of a single case in which the two active stages, larvæ and adults, occupy the same habitat and utilize the same kind of food. The nearest approach to it appears to be in some scavenger forms in which the adults and larvæ may both partake of the decaying material—in somewhat different condition, however; and the habitats of the two stages are very different. The blood-sucking habit is common for the adults, but the larvæ of these species have different habits. Even in the case of the obligate, parasitic, blood-sucking Hippoboscidae, the larvæ are nourished, not by the host directly, but within the parent fly. And in the few cases where the larvæ are blood-sucking (*Auchmeromyia*) the adults appear not to do so.

If one were to point to a single factor which has had most influence upon the life cycle of the Diptera it would seem to be the habits of the larvæ. This, as we shall see, determines to a large extent the habitat of the egg and it has likewise a profound effect upon the specializations and adaptations of the pupa stage and to a lesser degree upon the habits of the adult, particularly upon oviposition.

Certain prominent lines of specialization are familiar to all. There are the aquatic species with their host of specializations and adaptations in egg-laying, for the maintenance of the egg in this precarious environment, for the locomotion, defense and respiration of the larva; for the maintenance and preservation of the pupa and for the emergence of the adult.

There are the numerous parasitic species with the perfection of the instincts for locating prey, many unique contrivances for safeguarding the eggs, interesting adaptations which enable the larva to reach its feeding grounds and to maintain itself variously as an external, a subcutaneous, a gastric, an intestinal, a nasal, an auricular or a vaginal parasite.

There are scavengers of all degrees of specialization; there are fruit flies and leaf miners and gall-making species and borers in root and stem; each showing peculiarities not encountered in the other groups and each, indeed, far removed from what must have been the original structure and habit of the ancestral forms.

The species of aquatic, scavenger, or parasitic habits are free from the restrictions governing the development of those species dependent upon living plants, but the life-cycle of the gall-makers, leaf miners and fruit flies is often built around the annual cycle of the host plant and we find many nice adaptations for the utilization of the potentialities of the plant tissues by attacking them at the exactly right time in their development.

THE EGG.

The egg stage shows many adaptations to its environment and in anticipation of the welfare of the subsequent larva.

The adults lack a definite ovipositor of chitinous appendages yet the terminal abdominal segments may be adapted to insert the eggs into the softer tissues of plants, fruits, etc., as in the Tryptidae. Much more frequently the eggs are simply dropped, deposited, or glued to the surface of the substratum, on or in which the young may find nourishment. They may be (a) laid singly, (b) arranged in indefinite, irregular blotches or masses, (c) ranked with some definiteness but not fastened to each other, or (d) most carefully arranged in a definite manner with respect to each other, and fastened with a cement-like secretion. The cyrtid female expels the eggs forcibly in great numbers while hovering up and down a tree trunk (King*); conopids attach them to their host while in flight; sarcophagids will drop their young through a screen to food material some distance below. The interesting manner in which the female *Culex* holds the first few eggs upright between her crossed hind legs until enough can be fastened together to make the raft float has been described by Howard, et al.† Miall‡ describes some beautiful adaptations by which the eggs of aquatic Diptera are moored at the surface of the water. *Chironomus* eggs are laid in gelatinous ropes that are held in place by peculiarly twisted threads. The raft of *Culex* eggs floats by its own convexity, the single eggs of *Aedes* and *Anopheles* have curiously moulded air floats to decrease their specific gravity. The female ephydrid may crawl under water to fasten her eggs to submerged objects.

*King, J. L. Observations on the Life History of *Pterodontia flavipes* Gray, *In Annals Ent. Soc. Amer.*, IX, 3. Sept., 1916, 315.

†Howard, Dyar and Knab, *The Mosquitoes of North and Central America and the West Indies*.

‡Miall, L. C. *The Natural History of Aquatic Insects*.

All the eggs may be matured and extruded at one period, after which the female usually dies rather promptly. Among Leptidae and Simuliidae several females may contribute to the same egg-mass and their dead bodies are found together. Or the eggs may mature in definite batches at successive intervals. Or they may mature gradually and continuously and be laid over a period of several days as matured.

It is puzzling to explain certain indirect methods by which the larvae are obliged to reach their proper feeding grounds. The human bot fly, *Dermatobia cyaniventris* is said to lay eggs on the bodies of a mosquito which serves as the porter for transference to a warm-blooded host, the contact with which causes prompt hatching. The well-known cases of the common Oestridae in which the eggs are laid on a part of the body of the host remote from that occupied by the larva would seem to be a highly inefficient habit. The eggs of certain Syrphidae may be laid on plants in anticipation of the usual subsequent infestation by aphids on which the young depend.

The duration in the egg stage is extremely varied, ranging from as few as four hours in the case of certain Muscidæ to commonly two or three days, or as many weeks. There are cases in which the winter is passed in the egg stage; or, most remarkable, where an entire year and a second winter of dormancy may be followed by successful hatching, as in certain mosquitoes.

As a rule, a considerable number of eggs are developed, but this varies even in a single family like the Tipulidae from 45 to 2,000. Other species which are reputed to lay large numbers of eggs are certain Simuliidae, Cyrtidae, Trypetidae, Muscidæ, and Tabanidae. From the data I have noted it would seem that the average number of eggs per female is between 100 and 200.

THE LARVA.

The larval stage of the Diptera shows extreme specialization, being further removed from the typical arthropod condition than any other order. In the majority of the families this stage is a somewhat degenerated one and in many of them extremely so. True thoracic legs are always wanting and only rarely are pro-leg-like structures present. A definite head with well developed mouth parts and sensory organs is wanting in all the higher families. The condition of the spiracles also shows

great reduction, frequently only an anterior pair and a posterior pair or group remaining.

The moults seem commonly to be three in number. The exuviae are not as a rule prominent and often are entirely inconspicuous.

Organs especially adapting the larva to its environment are frequently noted. Curious suckers and pads for clinging to the surface of rocks in swift streams are exhibited by the Simuliidæ, Blepharoceridæ, etc. Peculiar stellate hairs for increasing surface tension are shown by *Anopheles*. One of the most interesting structures is the well known "rat-tail" or telescopic, posterior, breathing tube of certain Syrphidæ and Ephydridæ, which enables its possessor to feed from one to several inches under the water, while breathing air from the surface.

The majority of dipterous larvæ are aerial in respiration; Blepharoceridæ and Simuliidæ have tracheal or blood gills; while certain Psychodidæ have both open spiracles and functional gills; and the culicid larvæ accomplish respiration in part by spiracles, by gills, through the integument and per rectum.

Dipterous larvæ inhabit well-nigh every accessible haunt on the globe and feed on organic matter in every possible form.

Many are aquatic—Culicidæ, Simuliidæ, Blepharoceridæ and in part the Tipulidæ, Dixidæ, Chironomidæ, Rhyphidæ, Leptidæ, Stratiomyidæ, Tabanidæ, Ephydridæ, Sciomyzidæ, etc. Some of them prefer the clearest and swiftest of streams, others frequent open still water, some stagnant pools and some the foulest of liquids. In fact, practically every condition of water is utilized by some species of the single family Culicidæ. Certain chironomids are said to exist at depths of 1,000 feet.

The food of these aquatic larvæ is very varied and there is a definite correlation between the nature of the food and the specialization of head and mouth parts. Some devour micro-organisms, others small plants, as algæ, others small animals and some doubtless the decaying organic materials themselves. Many species live in the soil, especially in moist soil or mud. Their food is either other small animals (Tabanidæ), or the decaying organic matter which contaminates the mud (Syrphidæ), or the roots and tissues of plants (Tipulidæ).

A host of species are found in decaying vegetable or animal matter in every possible stage of disintegration (Psychodidae, Muscidae, Drosophilidae, Bibionidae, Mydidae, Asilidae, Heteronemuridae, etc.) We have all marveled at the adaptations which enable an ephidrid fly to live as a larva in pools of crude petroleum, a substance highly toxic to almost all insect life.*

Compared with the Coleoptera, Lepidoptera, Hemiptera, and Orthoptera, Dipterous larvæ are rarely phytophagous on living plants. There are comparatively few crop pests. Yet many are leaf-miners, a good many feed in fruits, seeds, etc., a number are borers in the cambium and other parts of the trunks and stems and some feed exposed on the surface. The Cecidomyidae or Itonididae are almost exclusively phytophagous and exhibit the most remarkable and intricate and inexplicable adaptations to the abnormal plant structures they occasion and to securing food.

The larvæ of many Tabanidae, Syrphidae and Asilidae are predaceous on insects and other small animals. Certain lepid larvæ are said to construct conical pitfalls for ensnaring prey, after the manner of ant-lions.

Many species of the Bombyliidae, Phoridae, Pipunculidae, Conopidae, Cordyluridae, Sarcophagidae and Tachinidae are parasitic on other insects. A few are parasitic on warm-blooded animals, the Hippoboscidae as ectoparasites, the Oestridae and in part the Muscidae, Sarcophagidae and Syrphidae as endoparasites. Certain species of the Muscidae are unique in having larvæ which are intermittent blood-suckers on mammals and birds.

THE PUPA.

One of the most noteworthy features of this order is the clever manner in which the last larval exuvium is utilized as a protection for the pupa stage. Cases aside from the Diptera may be cited where the larva retains its exuvia, more or less mixed with excrement, as a covering during the quiescent transformation period, but I know of none which approach the diptera in the perfection of this habit.

In the suborder Cyclorrhapha entirely and in many of the Orthorrhapha the last molt is not cast at all, but becomes

*See Crawford, D. L., The Petroleum Fly in California. In *Pomona Col. Jour. Ent.* IV, 2, May, 1912, pp. 687-697.

inflated and indurated around the pupal membrane to form a complete, waterproof and resistant box within which the pupa stage is secure. A pair of thoracic spiracles is projected through this puparium for the respiration of the pupa. Quite as unique is the adaptation by which, in several dozen families, an inflatable sac, the ptilinum, is projected through the frons to dislodge the cap from the puparium and permit egress of the fly. So far as it is possible to formulate rules, it is the rule for the pupa stage to be passed in or near the larval habitat. In the case of aquatic or semi-aquatic larvæ the pupa is found in drier situations nearby. It is adapted to float on the water in the Psychodidæ, Chironomidæ, Stratiomyidæ and Ephydridæ. It may even survive successfully on the bottom of pools (Chironomidæ), or under water in streams or lakes, as in certain Simuliidæ, Blepharoceridæ and Ephydridæ.

In the case of the parasitic species the pupa may remain in the host (Conopidæ) or leave the host and seek protection on the ground (Tachinidæ and Oestridæ). In the ectoparasitic Hippoboscidæ this stage may be glued to the hairs or feathers of the host or lie on the ground.

As to the duration in the pupa stage we note the same variation as for the other stages. As a rule this stage is a rather short one, exceptionally occupying only a few hours, and commonly from a few days to a few weeks. But it is very often utilized as a hibernating stage, and in remarkable cases a second winter may be passed in this condition (Trypetidæ). This tendency of part of the brood to be delayed over an entire additional year as exhibited by the eggs of certain mosquitoes and the puparia of some fruit flies is a most inexplicable adaptation for the preservation of the species.

The exact length of the pupa stage is seldom recorded because of the fact that a prepupal stage of most irregular length may occur after the puparium becomes indurated before the change from larva to pupa takes place.

In the matter of activity of the pupa certain families of the Diptera are remarkable. The mosquito pupa swims about actively and avoids enemies in a manner most remarkable for a stage traditionally quiescent.

THE ADULT.

The adult stage is usually short lived, but is quite variable in the different families, and may even vary greatly in the same species, depending on the success of mating, feeding, etc. It is believed that in some species (Culicidæ, Oestridæ, etc.) the adults normally live only a few days and many forms probably never feed. Others lead a very active and vigorous life for some weeks or months as Trypetidæ, Drosophilidæ, Anthomyiidæ, Muscidæ, Tachinidæ, Hippoboscidæ, etc. Certain adults have been kept alive well over a year.

Their haunts are almost as varied as those of the larvæ. Two conditions are especially favored:

- (a) The vicinity of water in which the immature live. Here are found many Tipulidæ, Dixidæ, Chironomidæ, Blepharoceridæ, Ephydridæ, Cordyluridæ.
- (b) Sunlight, which is especially effective on the activities of Tabanidæ, Syrphidæ, Bombyliidæ, Conopidæ and others.

The location of their own food is of course a dominating factor. The most noteworthy point regarding the food of adults is the complete specialization away from the primitive habit of defoliating plants. A very great number of species secure their food from flowers. The Tipulidæ, Culicidæ, Stratiomyidæ, Tabanidæ, Bombyliidæ, Syrphidæ, Conopidæ, Anthomyiidæ, Muscidæ and Tachinidæ, are generally flower-feeders on nectar, or pollen, or both. Many species can feed on liquid organic matter or dissolve solid substances and sponge them up.

Species of the families Blepharoceridæ, Leptidæ, Asilidæ, Therevidæ, etc., are predaceous on small insects. In two families, the Tabanidæ and Simuliidæ, almost without exception, the females suck the blood of warm-blooded animals. Six other families are known to contain blood-sucking species—the Culicidæ, Chironomidæ, Psychodidæ, Muscidæ, Leptidæ and Hippoboscidæ. In only one family, the Muscidæ, do we find blood-sucking males, the males of the other families generally feeding on pollen, nectar, etc. Some of the Muscidæ feed on blood drawn by other insects (not being capable of drawing blood themselves) by inserting their proboscides at the side of those of their piercing relatives. A curious habit is recorded

among the Hippoboscidæ, of individuals puncturing flies of their own kind and sucking the blood which the latter are drawing from the warm-blooded host. It is said that chains of these flies three or four individuals long may be found, taking the blood successively from their more fortunately (or unfortunately!) situated associates. The Hippoboscidæ are unique among permanent ectoparasites in possessing wings.

Blood appears to be especially effective on the development of the eggs. For example in certain Muscidæ several feedings of blood are necessary for the development of each batch of eggs. It is said that *Aedes calopus*, after feeding the first time, lays eggs and then becomes nocturnal in habit.

The mouth-parts of the adults, like those of many of the larvæ, are extremely specialized away from the ancestral condition. Within the family, however, they are, superficially at least, rather homogeneous; the species adapted for feeding in the several ways are hardly as diverse in structure as one would expect. The mouth-parts of the blood-sucking Muscidæ are probably unique among piercing insects in having the labium specialized as the cutting apparatus and adapted to enter the wound. The proboscis is rarely extremely elongated, an Indian tabanid having a beak an inch and a half long and three times the body length; this is probably used in probing flowers.

The number of generations a year varies in the Diptera from one, as in Oestridæ, certain Tipulidæ, Syrphidæ, etc., to two or three, which would seem to be the most common condition, (Tabanidæ, Cecidomyidæ, Sepsidæ, Syrphidæ, Tryptidæ, Anthomyiidæ, etc.), to 7 or 8 in certain Muscidæ, 8 or 10 in some Tryptidæ, Simuliidæ and Culicidæ, and as many as 20 in Drosophilidæ.

The number is determined (1) by a certain inherent *minimum* time for each stage in each species and (2) by environmental conditions of heat, moisture, food, etc.

It may be said that the dipterous life cycle is noteworthy for its *shortness in certain species*, rather than for any remarkable prolongation or slowness of development. The shortest complete generation is about 10 days for the house fly, fruit fly, etc. while a duration of more than one year is very unusual.

The method of passing the winter is an interesting problem, but unfortunately one on which we have little information.

Any one of the stages may be adapted for hibernation; perhaps more often the pupa, then larva, adult and egg in the order named.

There are many curious mating habits among the Diptera. A common habit is to pair while dancing in swarms. In several cases the males emerge a little earlier and then await the emergence of the females, as in Simuliidae and Tipulidae. Indeed, the tipulid male is said to assist the female from the puparium. Oestrid males await about the host animal for the approach of the females. Secondary sexual ornaments of dolichopodid males are displayed before the females; while certain Empididae construct frothy balloons to attract the females. In the Syrphidae I have noted mating while hovering, (both facing the same way, male uppermost), and while resting on leaves, facing in opposite directions. In the latter case it may continue uninterrupted for two or three days (*Temnostoma* spp.)

In methods of reproduction we find a very great range. Parthenogenesis seems not to have been developed in this order. Ordinarily, fertilized eggs are laid in the usual way. The Sarcophagidae are all larviparous or oovoviparous. The eggs hatch *in utero* and the active larvæ are extruded, in this family often being attached to a grasshopper or other host while both insects are in flight. The number of offspring per female in this family appears to be very high.

In the *Glossina* and Hippoboscidae we find a remarkable condition, analogous to the vivipary in mammals, in that the larvæ derive all the nourishment for their growth and development from special glands in the uterus of the female. This, of course, reduces greatly the potential number of offspring; there are only six or eight per generation in the sheep tick.

Another remarkable condition known as paedogenesis is described for Miastor of the Cecidomyidae. It is said that eggs are produced in ovary-like organs of the larva. These hatch and the young larvæ remain in the abdominal cavity feeding on larval parent tissues until they finally escape. A series of such multiplications is followed by pupation and a normal sexual reproduction of adults. The pupa of a species of *Chironomus* also reproduced parthenogenetically, according to Grimm.

8. HYMENOPTERA.*

By T. D. A. COCKERELL, University of Colorado.

In discussing the life history of the Hymenoptera, we naturally turn more especially to those problems which center about metamorphosis on the one hand, and parasitism on the other. My work on fossil insects has caused me to speculate on the origin of these habits and characteristics, without enabling me to reach any definite conclusion. To many, these speculations will doubtless seem rather futile, yet no intelligent person travels a road without some thoughts about his journey's end. Hypotheses not only quicken the imagination, but at once increase the significance of every scrap of information which tells for or against the opinions one has formed. Thus the discovery of a fragment in some ancient rock becomes a dramatic event.

Overlooking the town of Boulder is a hill from which one can look north across the flank of the front range. A series of red rocks, now standing on edge, once formed the shore of the Upper Carboniferous sea. A narrow valley separates these from another sharp ridge, belonging to the lower part of the Upper Cretaceous. It is interesting to look at these strata and realize that in the interval between the first and the second, the typical flowering plants, the birds, the mammals and the insects with complete metamorphosis all came into existence. Were these striking events accidentally coincident, or was there some causal connection between them? The sea was the mother of life and the land was discovered, so to speak, by successive types of organisms. During the Carboniferous, the terrestrial arthropods, especially the insects, were abundant and often of immense size. The Amphibians represented an invasion of the vertebrates, doubtless preying upon the rich insect fauna. Reptiles, with hard-shelled eggs, finally solved for the vertebrates the problem of completely terrestrial existence. Birds and mammals must have owed the possibility

*I took part in the symposium as a substitute for another, to whom the topic had first been assigned. I prepared no manuscript, and indeed have no special knowledge of the matters which I should have discussed. It has not seemed worth while to compile a summary from the literature, in order to secure approximate uniformity of treatment.

of development largely to the abundance of insect life. Thus the insects, at first comparatively immune from attack, were hard pressed by enemies on the ground, in the trees and even in the air. The larger, more conspicuous types disappeared, giving place to a great variety of rather small forms, which could easily be concealed, or were perhaps in some cases, extremely prolific. In the meantime the increasing diversification of the flora, with the development of many kinds of woody plants, afforded new opportunities for specialization. The advantages of metamorphosis under these conditions are obvious and no one can doubt that several distinct types of larva began to diverge from the primitive orthopteroid condition, in the soil, in the water, and within the tissues of plants. It thus seems to me probable that the primitive Hymenopteron did not possess a caterpillar-like larva, but a boring one, in the manner of the existing Siricoidea. Such a larva would be in a position to take advantage of the newer types of vegetation, and at the same time avoid to a large extent the attacks of vertebrate enemies. The birds of those days had teeth, and the bill as a boring organ, such as we find in the woodpecker, had not developed. This view is supported by the only well-known Mesozoic Hymenoptera, the Pseudosiricidae. These large insects, as I have lately shown, survived into the Eocene, but are now extinct. They possessed what is to be regarded as a stout ovipositor, probably derived from an orthopteroid ancestor. Their venation does not lend any support to the idea that the basal nervure is a cross-vein; it should rather be a branch of the cubitus fusing distally with the media. From such a type, it is not difficult to derive on the one hand the Ichneumonoid parasites, and on the other the ants. The resemblance of the venation of the Pseudosiricidae to that of the ants is so striking that they were once regarded as gigantic ants. Just as the New Zealand parrot, from feeding on vegetation, has taken to attacking sheep; so the early Hymenoptera, successful as borers in wood, may have taken to boring in various larvæ, securing thereby more elaborated, more concentrated nourishment for their young. The ants, on the other hand, met the problems of life in another way, by developing community organization. The ant larva is a highly specialized being, which has to be fed by the adult. Is there not reason to suppose that it was originally self-supporting, and was therefore in pre-ant times a borer in

vegetable tissue? That it fed externally in the manner of a modern sawfly seems in the highest degree improbable.

It is obvious that parasitism has arisen over and over again among the Hymenoptera, as Wheeler* has recently shown in some detail. The parasitic aculeata have nothing to do with the Ichneumonoidea or Chalcidoidea, and the inception of their parasitic habits was entirely different. Among the bees, the extraordinary case of *Androgynella* is very suggestive.† This type, of which two species are known, is a *Megachile* in which the ventral scopa is wholly lacking in the female, which has 13-jointed antennæ and spined anterior coxae, as in a male, but still retains the sting. In the light of modern genetics, we can form some idea of the origin of such a condition, but that it should be able to survive is surprising. It could survive only by becoming a guest or parasite of the other or normal bees, and this is evidently what has taken place. Thus parasitism among bees may owe its origin to a species of necessity, confronting insects which no longer possessed the power to function in the ordinary way. Among the Ichneumonoidea it was rather the development of an advantage, leading to a great increase in the number of genera, species and individuals. The parasitic aculeata have never been dominant like the ichneumons; they are mostly comparatively rare or sporadic in their occurrence.

These considerations suggest interesting possibilities of experiment. How far is it possible to modify the reactions of insects by changing their conditions of life? But when the modification is internal, is due to some alteration of the germ-plasm, it may well affect instincts as well as structure. Modern breeding, such as that of *Drosophila*, has revealed the fact that, at least in certain insects, mutations are relatively frequent. In nature, no doubt, the vast majority perish, but an occasional one survives and enters upon a new course of life. Thus a process which is detrimental to many individuals, is advantageous to the group, being in the long run a potent cause of specific and generic differentiation. The outcome is diversity of adaptation, purposeful in the sense that the existing powers of variation and response are capable of leading to the results we see.

*Proc. Amer. Philosophical Society, LVIII (1919), pp. 1-40.

†For details, see Philippine Journal of Science, XIII, D. 4 (1918), p. 140.

9. THE LIFE CYCLE OF INSECTS; GENERAL DISCUSSION.

STEPHEN A. FORBES, Chief, Natural History Survey of Illinois.

In preparing for a general discussion of so large and complex a subject as that of this symposium, two choices were open to me. For one, I might have tried to summarize, generalize, and reduce to fundamental principles as well as I could on the spur of the moment the data and inferences presented by the specialists who have entertained and instructed us by their remarks on the life cycles of the various orders in which they have specialized. The alternative choice was a presentation and brief discussion of a limited number of topics, too general to come within the divisions of our subject treated by my predecessors on this program, and of kinds to which, in my judgment, we ordinarily give too little attention. Whether rightly or wrongly, I have made this second choice, with the idea especially of pointing out deficiencies in our knowledge by way of suggestion to the younger entomologists who are in the line of succession to the problems which we of the passing generation have solved imperfectly, mistakenly, or not at all.

One of the most fundamental features of the life history of insects, with its innumerable variations more or less adaptive in character, is the necessary inference that all these fixed differences are predetermined in the protoplasmic composition and structure of the fertilized egg, each succeeding step in any life history following upon the preceding one by a physical necessity; and the further fact that in each order of insects—each insect species, indeed—this minute, invisible, and possibly indeterminable structure of the protoplasmic egg must have been passed down by inheritance virtually unchanged from an extremely remote ancestry. On the other hand, all the variations and differentiations which have arisen to distinguish species from species, family from family, order from order, in respect to the general course and the minor details of their life histories, must have made their appearance as variations and differentiations in the egg protoplasm, which exhibits at once a constancy in some lines and an instability in others which, taken together, have made evolution possible. This *constancy*,

we see illustrated by the fact that the average course of the life cycle in any insect species is virtually uniform so long as the external conditions affecting it are uniform. The average lengths of the egg, larva, pupa, and imago stages of a holometabolous species are the same in any given locality, season after season, if the seasons average alike in temperature, humidity, etc.; but the *instability*, nevertheless, of this same protoplasm is shown by the fact that individual variations in the details of life history appear among insects of the same species and variety, hatched from eggs laid on the same day, and kept continuously under identical conditions. In Doctor Shelford's unpublished experiments, pupæ of the codling-moth, formed on the same day from the same lot of larvæ and kept side by side under the same conditions until the imagoes emerged, have had pupal periods of $9\frac{1}{2}$ days, $10\frac{1}{2}$ days, and $12\frac{1}{2}$ days in one series, and in another series of $10\frac{1}{2}$ days, 11 days, $11\frac{1}{2}$ days, $12\frac{1}{2}$ days, and $13\frac{1}{2}$ days, and so on; and another colleague, Mr. P. A. Glenn, tells me of 24 codling-moth pupæ formed on the same day and treated precisely alike, of which one gave the imago in 8 days, six gave imagoes in 9 days, ten in 10 days, six in 11 days, and one in 12 days. Still more significant are some of his data concerning the incubation periods of the eggs of the codling-moth, these varying from 12 to 15 days for a lot of 46 eggs laid May 5, from 8 to 10 days for 162 eggs laid June 3, and from 8 to 11 days for 118 eggs laid June 5, all being kept under like conditions. He has had, indeed, occasional instances of single larvæ of the first spring generation surviving as pupæ until the following spring, representing thus a one-generation variety of the codling-moth, although their brothers and sisters took the usual course of two or three generations in the year.

These individual differences in the sensitiveness of the egg protoplasm to the stimuli of development furnish, if they are heritable, abundant materials for the action of natural selection in fitting a species more exactly to its environment in respect to its life history, just as other kinds of variation make possible an improvement of its structural adaptations; and a study of these variations in life history, of their continued heritability, and of their advantages and disadvantages to a species by way of its adaptation to the various environments in which it is found, is just as necessary to a knowledge of our subject as is the

corresponding study of visible variations of structure to a knowledge of the phylogeny of the insect organism.

One of the environmental conditions to which an insect may adjust itself by reason of this flexibility of its life history is its relation to its food-plant and to its competitors for food. Remembering that the prosperity of a plant-feeding insect is dependent on the abundance and continued growth of its food-plant, and that this plant, for its own best prosperity, must produce for its insect guests timely supplies in quantities which can be spared without actual injury to the plant itself, we see a mutual advantage to insect and plant alike if the draft on the growing plant shall be distributed over as long an interval as possible, in order that the product of continuous growth may go as far as possible to supply the demand. Obviously, the demand of a thousand insects delivered in one day might effectually bankrupt a plant which could honor the draft without embarrassment if it were distributed over a fortnight or a month; and this advantage to the food-plant would react, of course, to the advantage of the feeding insect also. There is thus a standing reward offered to every insect dependent for food on a living and growing organism, for establishing and maintaining an individual variability in its sensitiveness to stimuli such as shall lengthen the period of its depredation.

Of course, individual differences in the rate and the period of development of the insects of the same generation, and even of the same parentage, are not all due to variations traceable to the egg, but many are consequences of different individual exposures to stimulating or retarding factors; as a consequence of them all, (some original and some incidental), the effect of an infestation is diluted and diminished by an extension of its period, to the common advantage of the infesting guest and the infested host.

Furthermore, it seems possible that this depredation period may be shifted as a whole, so as to come earlier or later in the season, if competition with another species of kindred habit may be thereby evaded. If two species infest a food-plant at the same period, their joint number must be so limited, as a general rule, that their attack will not destroy the food-producing plant; but if they can come to succeed each other so that each shall have the plant for a time to itself, both may maintain a higher rate of multiplication without permanent

injury to their common host; and individual variations in the length of the stages of the life cycle already referred to make this easily possible. If there is any initial difference whatever between the competing species as to the period of their attack, natural selection may do the rest, and even if there is not, mutation of habit may have the same effect. I happened, many years ago, upon an apparent instance of this kind, when I was studying the life histories of the so-called root-worms of the strawberry—larvæ of three species of chrysomelid beetles which devour the roots of the plant. One of these larvæ, that of *Colaspis brunnea*, begins its work in southern Illinois in early spring and continues active through June; another (*Typophorus canellus aterrima*) begins in June and continues into August; and the third (*Graphops nebulosus*) begins in August and continues active through the fall, hibernating, in fact, in the larva stage.

It is a significant fact that another species (*Graphops pubescens*) closely allied to the last and with a like distribution, but living on another food-plant, refusing, indeed, the roots of the strawberry and feeding only on those of the wild evening primrose, has a very different life history from its near relative, wintering as an adult instead of a larva, as does the strawberry species. There is here a suggestion of a possible shifting of the life history of the strawberry *Graphops* in a way to adjust its demands for food to those of its competitors. Of course, this seeming adjustment may have been a coincidence merely, and I do not know of another instance of the kind; but, on the other hand, I do not know that such instances have been sought. Most of our best life history work has been done on insects infesting the crop plants, where the natural reactions of plant and insect are so generally disturbed or annulled by the overpowering agency of man that we must look for clear cases of interlocking life histories of competing insects among those dependent on uncultivated plants; and here but little has been done.

The foregoing case may at any rate serve to illustrate the fact that for a full understanding of the adaptations of insects to their environment by way of their life histories, we must not study merely the separate species in their natural habitats, but must make local ecological groups our units for investigation, and inquire into the system of competitions, and adjust-

ments and avoidances of competition, exhibited in their relations to each other. We have much reason to expect, indeed, that an insect association of long standing in a geographical area, or in a set of situations of fairly uniform character, will have come to make many internal readjustments—adaptations of one species to another in habit and life history, of each species, perhaps, to several others, of different stages of the same species each to the other, such that the whole association may avail itself to the best advantage of the resources for existence and multiplication offered to it by any environment. The strains and pressures of competition will thus be in some measure relieved, and an internal equilibrium of the ecological group will be reached which will smooth and steady the system of interactions within the association, to the general advantage of all its members. It seems to me quite possible that a single species of wide range may have become a permanent member of unlike associations in different parts of its area of distribution; may have had to adjust itself, consequently, to different systems of interaction with its associates; may have acquired local peculiarities of life history not to be understood until these internal systems have been studied and made out.

The subject is, indeed, delightfully complex—a challenge to the curiosity and ingenuity of the accomplished naturalist equipped with apparatus for exact experiments with variations of temperature, moisture, light, rates of air movement and evaporation, such that he can produce any desired combination of these natural factors of the insect environment and determine their separate and conjoined effects on the life cycle of any species which he wishes to study in detail.

An equipment of this description is invaluable in testing the inferences of the field observer and in detecting reactions to features of the insect environment which are obscured or lost in the complex of the natural system out-of-doors. By such a means we are beginning to account for some, at least, of the almost explosive outbreaks of insect multiplication in certain species, which we find peculiarly sensitive to meteorological conditions by which others are little affected. Doctor Shelford tells me, for example, as a result of his studies now in progress on the chinch-bug, that these insects, whose numbers fluctuate enormously in successive years, are extremely dependent on relatively high temperatures; that with optimum

humidity, multiplication is very slow and breeding experiments usually fail at a temperature of 70° F. (a much higher limit than that of any other insect studied), but that with high humidity and high but variable temperatures like those of a hot, moist day in summer, breeding experiments are highly successful, and the rate of multiplication is almost unbelievably rapid.

I am beginning to hope that, by vivarium work and companion studies in the field, we shall be able soon to standardize our life history data so that we can describe the life cycles of insects, not primarily in unreliable units of time, so variable as to be perplexing, but in ecological units of temperature, humidity and the like, invariable for a species whenever and wherever it may be found. An example of such a standardization is furnished by the product of recent work on the life cycle of the codling-moth done by Mr. Glenn at a well-equipped orchard station in southern Illinois, to the effect that in normal seasons, when the sum of all mean daily temperatures which fall between 50° and 85° F. reaches 550°, the eggs of the spring generation of the moths will begin to hatch, and when these totals reach 1550° those of the second generation will hatch, and when eleven hundred degrees is added to this sum, the third generation may begin to hatch; but that if this last total of 2650° is not reached before September 10, there will be no third generation at all in that year; and these statements may be expected to hold good every year without regard to the character of the season or to differences of elevation or latitude. Dr. Shelford is now working out in the vivarium a scheme of corrections to be applied to this forecast whenever the humidity factor is practically important.

Our present method of describing life histories in days or hours for each stage or phase is, indeed, thoroughly illogical, for mere lapse of time has, of course, no effect in itself; it is only the dynamic content or accompaniment of the time unit, especially in temperature and humidity, which really signifies. We must find our unvarying ecological constants and make up our life-history calendars of these and not of the uncertain units of time which we now use simply because they are the most easily obtainable.

Perhaps we shall never know just how and to what immediate profit the holometabola were differentiated, but that the

differentiation was a fortunate one for the future of insect life in the world is shown by the present great predominance of holometabola over ametabola and hemimetabola, and by the obvious advantages which they have in the struggle for existence. By their premature hatching from the egg before the characters of the adult have been laid down in the embryo, their larvæ are much more capable of adaptive modification for their life as larvæ than are young Orthoptera or Hemiptera, already virtually adult at birth, except as to size, sexual organs, and organs of flight. Hence we see, in the vast majority of cases, the holometabolous larva taking its own course in its own interest, quite regardless of the coming necessities of the adult, with the result that larva and adult have widely different ecological relations, belonging, indeed, to different ecological associations, and do not compete with each other in any way. As the closest competitors of an ametabolous insect are the members of its own species, the division of any species into two non-competing groups diminishes by a certain considerable fraction the dangers of this interspecific competition. On the other hand, the fact that the holometabolous insect must alternate between two quite different environments, one for the larva and the other for the adult, makes its failure to find either one a fatal catastrophe, requires the coincidence of two favorable environments, instead of the occurrence of only one, for its survival; but this danger is largely overcome by the remarkable development of instinct which leads the female adult to deposit her eggs at a place and time as favorable as possible to the success of the larva; and in the social insects it is of course much more than compensated by the solicitous care which the young of all stages receive from the mature.

I think we may also count the holometabolous insect as relatively fortunate in respect to its exposure to predaceous enemies, parasites, and contagious diseases. A grasshopper is endangered during its entire life cycle by the same kinds of destructive agencies—the same species of predators (except as it outgrows some of them), the same kinds of insect and other animal parasites, and the same bacterial and other fungous diseases—but white-grubs and May-beetles differ one from the other almost completely in these respects. The attacks of parasites and contagious diseases commonly increase in intensity with the length of time during which their victims are exposed

to them, so that they are much more destructive in the second half of the insect life cycle than in the first; but in a holometabolous insect with unlike larval and adult habits and habitats, this period is divided into two unlike periods of disease or infestation, and there is no second half to either of the two.

The multiplication of seasonal generations in some species is a consequence of a high degree of sensitiveness to temperature and other developmental stimuli; and this may enable a species to push its range into colder latitudes than would otherwise be possible, giving it at the same time a capacity for multiplication in the milder latitudes far in excess of that of its single-brooded competitors and enabling it to take prompt advantage of seasonal conditions temporarily favorable and to rally quickly from the effects of those temporarily injurious. I surmise that the many-brooded species have, as a rule, had an experience of frigid or semi-frigid life—that of a glacial period, for example—during which variations towards a quick physiological sensitiveness to heat stimuli have been selected for survival. Entomologists are but just beginning to determine accurately the so-called physiological zero or threshold of development of the several insect species, and have accumulated as yet too little precise knowledge of the temperature at which development begins and of the effects of differences of humidity in shifting this zero up or down to enable us to base our surmises on experimental evidence. There is an almost limitless field for interesting investigation open to those who have command of a good experimental equipment, and the entomologist who first carries through a seasonal series of experiments on the army-worm with its three annual generations in comparison with one of the single-brooded noctuids, both kept together under identical conditions for a study of their differences of reaction to ecological factors, will get some new and important results.

As I piece together, after a fashion, these few scraps and fragments of observation, interpretation, and inference which I am offering here, it seems to me that the general pattern which they suggest is that of a wide-ranging, open-minded survey of insect life as it is actually lived by these complex and variable creatures, in constant interaction with the still more complex and similarly variable system of objects and energies which together constitute the insect's world—that we need to

study that world from the insect standpoint as its center, to realize as clearly as we can, by insight and imagination, what it would be to a beetle or a butterfly, a caterpillar or a grub, if it were endowed with our capacities of observation, analysis and inference; how and to what ends and by what means it would act upon that world and how and by what means its world would react upon it in turn; and what has been the history of the system of actions and reactions through the agency of which it has become what it finds itself to be. Except as we can approximate this ideal—in so far, that is, as we adhere in our studies to the merely human point of view—our perspectives must be distorted and our emphases wrongly placed, to the confusion and disappointment of our efforts to solve the intricate problems of insect life.

THE EXTERNAL ANATOMY OF ANTHOMYIA RADICUM Linn.*

(Diptera, Anthomyidæ).

By HOWARD L. SEAMANS.

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- Abbreviations for Figures.
- Explanation of Plates.

The North American Anthomyidæ, though belonging to one of the largest and most important of the families of the Diptera, are nevertheless in very unsatisfactory condition from the systematic standpoint. The permanent work that has been accomplished on these flies has been concerned largely with the economic relationships of individual species, and, in this country at least, very little thorough work along taxonomic or morphological lines has been done. It is apparent that there is a real opportunity for systematic work in this group, and, as a preliminary step in this direction, the writer undertook a morphological study of *Anthomyia radicum* Linnaeus, one of our most common species in this family, and this paper gives the results of this study.

*Contributed from the Entomological Laboratories of Montana State College.

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Specimens for study were first softened in a solution of alcohol, glycerine and formalin. For the study of the wings and legs these parts were removed from softened specimens and placed in 70 per cent alcohol, then in carbolic acid-turpentine clearing solution, and finally mounted in Canada balsam. For the study of the body parts bearing sclerites and sutures it was usually necessary to cut away the parts with a sharp scalpel, boil in a 5 per cent solution of potassium hydroxide to remove non-chitinous tissue, preparatory to mounting in balsam. The head capsule was prepared in the same manner and mounted whole in balsam, in a xylonite ring. Treated in this manner the parts under study retained their normal form, while the bristles, sclerites and regions could be distinctly seen.

Some specimens were placed in chlorine water until they had been bleached to a light yellow and were almost transparent. These were then washed, dehydrated and placed in thin balsam until they were completely filled with the medium. Whole mounts were made in xylonite rings and studied for the various structures.

Drawings were made from prepared slides with the aid of apparatus consisting of a small arc lamp the light of which was directed through the barrel of a microscope placed horizontally with a mirror attached so as to present a surface to the ocular at 45°. When a slide was placed on the stage of the microscope the image was projected on a paper under the mirror on the table where it could be traced.

ANATOMICAL STRUCTURE.

The terms used in designating special sclerites, sutures or regions are for the most part those recognized by Dr. Crampton of the Massachusetts Agricultural College. In some instances terminology has been taken from Lowne, or other authentic sources, but since the terms are in common usage, they should cause no confusion.

THE HEAD.

The outline of the head when viewed from the front (Figs. 1 and 2) is nearly circular, being slightly wider than high, and less regular in the female than in the male. Viewed in profile the outlines differ greatly in the two sexes. In the female (Fig. 3) the line from the vertex to the base of the antennæ is almost at right angles to the line from the vertex to the occipital foramen. The face is almost perpendicular, having a slight tendency to be retreating. The antennæ are situated distinctly above the middle and are about one-third as long as the major axis of the head. In the male head (Fig. 4) the vertical angle is decidedly acute, the antennæ are situated at about half way down from the vertex, the face is retreating, making the epistome appear to protrude, and the minor axis is only two-thirds the length of the major axis. The posterior aspect of the head is essentially the same in both sexes, showing distinct sclerites and sutures, while the anterior portion shows regions which are variable in the two sexes. There are five sutures arising from points on the occipital foramen (Fig. 7). Two of these arise from the two dorsal angles of the foramen, two from the two ventral angles, and one from the middle of the dorsal margin. The two sutures arising from the dorsal angles of the foramen are the paracephalic sutures of Lowne (prsu). These extend upward to the vertex and then around the compound eyes. The two lateral halves of the head thus formed are the paracepala (prc) (Fig. 7).

The suture which arises from the middle of the dorsal margin of the occipital foramen extends about one-third the distance towards the vertex and forks, each fork disappearing in a faint, almost indistinguishable suture which turns downward at an acute angle to meet the foramen at the base of the paracephalic sutures. The two triangular areas thus formed are the epioccipital sclerites of Lowne (epos). The space between the paracephalic sutures and above the epioccipital sclerites is the epicephalon (epc).

The two sutures which start from the ventral angles of the foramen are the basal sutures (bsu). These extend downward, meeting a fold just above the oral margin, and become indistinct. The somewhat irregular six-sided area cut off from the paracephala by these sutures is the metacephalon (mte). The

vestiture of the occiput shows more or less distinct regions of which one is very clearly defined. This is a region just back of the compound eyes, the posterior eye orbit, set off from the rest by a row of more prominent hairs (Figs. 3, 4 and 7). There is a small patch of fine bristles at the base of each epioccipital sclerite, while the epiccephalon is bare, except for the post vertical bristles. The metacephalon is divided into two lateral regions by the vestiture, leaving a groove in the center practically bare.

Viewing the head from the front (Figs. 1 and 2) the most striking difference between the sexes is in the compound eyes. Those of the male are very large, being practically contiguous for a short distance, while in the female they are smaller and widely separated. The antennæ of the female are located higher up than are those of the male, and the vertical bristles are much larger. Except for a considerable narrowing in the male the regions in both sexes are homologous. The male head bears more bristles than the female but they are weaker and less prominent.

At the extreme vertex of the head in both sexes there is a heavily chitinized, slightly raised, almost equilateral triangle, with its apex directed towards the base of the antennæ. This is the ocellar triangle (ot) and it bears a simple eye in each corner. It bears three or four pairs of stout short bristles, the posterior ones upright, and the anterior ones directed forward. Below the ocellar triangle and above the base of the antennæ is a region known as the front. In the males this is a triangle with the apex directed upward and is known as the frontal triangle (ft.) (Fig. 2). In the females the front (f) is broad, somewhat rectangular, bears a pair of bristles located just below the ocellar triangle, and directed forward, the cruciate bristles. In the male these two bristles are located very close together at the apex of the frontal triangle.

The vertex in the female bears two pairs of large vertical cephalic bristles, the inner pair convergent and the outer pair divergent. Behind the ocellar triangle is a pair of divergent post vertical bristles.

On each side of the front, bordering the compound eyes, is a narrow region which reaches from the vertex to the base of the antennæ, where it is cut off by an oblique division line. These two areas are the parafrontal plates (prf) bearing eight pairs of

bristles in the female, and ten in the male, the fronto-orbital bristles (fobr). Below the parafrontal plates are narrow regions which follow the orbit posteriorly. These regions are the genæ (g) and bear no bristles or spines (Figs. 1, 2, 3, 4), but are sometimes pubescent.

At the base of the front and just above the base of the antennæ, is a triangular opening lunule (l) through which an eversible sac, the ptilinum, protrudes when the insect is emerging from the pupa. From this opening a suture extends downward on each side, ending just below the tip of the third joint of the antennæ. The eversible sac extends the entire length of the suture. This suture is the frontal suture (fsu) of Lowne, and a slight line of demarkation extends from the tip of the suture to the oral margin. The lower margin of the lunule is formed by the upper margin of the sclerite which bears the antennæ. (Fig. 5). The sclerite is cut off from the head capsule by a suture, for the most part concealed by the antennæ. This suture, however, follows the vibrissal ridge, below the antennæ, and then encircles the oral margin. The sclerite shows distinct regions including the epistome, though no bristles are present, and corresponds closely to the face, as that term is used by Lowne. However, Lowne includes in his term face all the area surrounded by the frontal suture. The area which Lowne considers the facialia or facial edge of the paracephalon is the region which in this species lies between the face and the frontal suture and bears the oral vibrissæ and facial bristles. (Figs. 1, 2, 3 and 4).

Between the genæ and facialia is a somewhat flattened, triangular area extending from the oral margin to the eye border. This is the transverse impression or bucca (bu) and in both sexes is devoid of bristles or hairs, but is somewhat pubescent. (Figs. 1, 2, 3 and 4). Bounding the bucca posteriorly and extending towards the occiput and along the oral margin is a distinctly raised or convex region, which is the cheek (c). This is covered with long black hairs and has a row of distinct bristles along the oral margin. (Fig. 1, 2, 3, 4).

The antennæ present no distinct sexual differences. (Fig. 6). They are three jointed, the third joint bearing a long, slender, pubescent, three-jointed arista (ar). The first joint of the antenna is the smallest, short, collar-like and slightly compressed laterally. There are two bristles on the anterior

surface. This joint appears to be immovably attached to the head. The second joint is longer, attached to the first by a movable joining, and bears a coronet of bristles on its anterior surface. The third joint is the largest, being twice as long as the second, somewhat broader, and laterally compressed. It is attached to the second joint by an immovable attachment formed by parts fitting together like saw teeth. In addition to the three jointed arista, this joint bears structures which are apparently sense organs, consisting of openings leading to small internal cavities. Each such opening is protected by a ring of bristles pointing outward towards a common center. This joint also appears to be porous and sponge-like, the pores being much smaller than the openings to the sense organs. All three points are covered with short, fine pubescence.

The arista (Fig. 8) is three jointed, all the joints movable, and pubescent. The first two joints are short, cylindrical, the second about twice as long as the first. The third joint is long, somewhat larger at the base and for the basal third, tapering from there to a fine hair-like point. The spines appear to be different from ordinary spines and may function as sensory hairs.

The discussion of the mouth parts will be left for a later publication as they appear to show no characters of value to this work, but do show some interesting anatomical features that need further study.

THE THORAX.

Of the thoracic segments, the first and last are greatly reduced, the mesothorax forming the greater part of the whole. The dorsum of the thorax, with the exception of the two anterior swellings, is the mesonotum. The two anterior swellings or the humeral callosities (hclv) are the upper portions of the pronotum. (Figs. 10 and 12). Anterior to the base of the wings a suture crosses the mesonotum, the transverse suture (trs), which separates the anterior region or prasectum (prs) from a posterior region, the scutum (sc). Above the halteres another suture crosses the mesonotum separating the scutum from a posterior, somewhat triangular region, the scutellum (scl). (Figs. 9 and 12). The mesonotum bears two distinct rows of large, strong bristles which diverge slightly posteriorly (Fig. 9). Each row consists of five bristles arranged two on

the praescutum, and three on the scutum. These are the dorsocentral bristles, those on the praescutum being the anterior dorsocentrals, and those on the scutum being the posterior dorsocentrals. Between the rows of dorsocentral bristles are two rows of setæ, never very symmetrical, variable in number, starting with two strong bristles on the praescutum and ending in two strong bristles at the posterior end of the scutum. These are the acrostichal bristles (acr). Two strong bristles are present on the humeral callosities, which are known as the humeral bristles (hb). (Figs. 9, 10 and 12). On each side of the praescutum, close to the humeral callosities, is located a strong bristle, the posthumeral bristle (phm.). Near the posterior angle of the praescutum there is a strong bristle, the praesutural bristle (prsl). On the sides of the praescutum, next to the notopleural suture there are two strong bristles, the notopleural bristles (npl). (Fig. 12).

In addition to the bristles mentioned above, the scutum bears two bristles outside of each row of dorsocentral bristles, the intra-alar bristles (ial). Below and somewhat anterior to the intra-alar bristles, on the sides of the scutum, are located the supra-alar bristles (sal). In some of the Anthomyiidae there are three supra-alar bristles, the anterior one being the "Pro" of Stein. Posterior to these and located on the side and dorsum of the postalar callosities, are the post-alar bristles (pal).

The bristles of the scutellum are small except for one pair of strong bristles located at the anterior angles of the scutellum, and a pair of still larger ones, located on the posterior border of the apex. This last pair have been called the apical bristles or scutellar apicals (scla).

The prothorax is indistinct when viewed from the side, being represented by three visible sclerites. Of these three, the pronotal lobe, or humeral callosity, is the most conspicuous (Fig. 12). This is an irregularly shaped sclerite somewhat resembling a budding mushroom in general outline. The two humeral bristles (hm) are located on this sclerite, near the dorsal margin. Below this sclerite, and separated from it by a distinct suture, is the proepisternum (pres). This is also irregularly shaped and bears three bristles near its ventral margin, just above the base of the prothoracic coxa. Anterior to these two sclerites another sclerite can be noticed in a lateral view. This is the prodorsum (pd) of Lowne, but it can be better studied in an anterior view.

The anterior view of the prothorax (Fig. 10) shows the parts before mentioned. The prodorsum forms the dorsal rim of the foramen and an articulation with the head. At the two lower angles of the foramen are triangular sclerites, which have anterior projections. These are the condyles (cnd) of Lowne and also articulate with the head. Between the condyles is a rounded somewhat shield-shaped sclerite, which Lowne has termed the sella (s). This articulates with the lower part of the occipital foramen of the head.

Below the sella and condyles and between the coxa (cx) the prosternum (psn) is seen as a somewhat shield-shaped sclerite, but extends posteriorly to meet the sternopleurite. A study of the pleura of the thorax shows many sclerites and sutures of the other thoracic segments (Fig. 12).

Posterior to the propleura and below the praescutum is a large, irregular-shaped sclerite, the largest of the pleural sclerites, which is separated from the posterior portion of the mesopleura by a strong suture, the pleural suture (plsu). This suture, arising from the base of the wing, extends irregularly to the middle coxae. The sclerite formed by this suture is made up of the mesoepisternum fused with part of the sternum and proepimeron. The sterno pleural suture (ssu) imperfectly divides this sclerite dorso-ventrally, the dorsal portion being the anepisternum (ans) and the ventral portion the sternopleurite (stp). In the upper anterior corner of the anepisternum is located the anterior spiracle (spa) (Figs. 10 and 12). Behind the upper portion of the pleural suture is an irregularly pentagonal sclerite, which has a short suture starting into it from the dorsal border near the wing base. This suture indicates the fusion of two sclerites, the anterior one being the pleural wing process (pwp) and the posterior one the ptero-pleurite (ptp). Below the ptero-pleurite and behind the lower section of the pleural suture is located another irregular five-sided sclerite which is divided by two faint sutures into three parts. The whole sclerite is known as the mero-pleurite and forms the posterior ventral sclerite of the mesothorax. The posterior dorsal sclerite of the mesothorax is located in front of the halteres, and divided into two portions by a slight transverse suture. This sclerite extends to the anterior portion of the scutellum, and is known as the pleurotergite (ptg).

Immediately below the scutellum is an exceedingly convex sclerite, part of the post-scutellum, which extends laterally to the pleurotergite, and is known as the mediotergite (mdtg). Below the mediotergite is a sclerite which bears the halteres, the metanotum (mtn). Back of the meropleurite is a long, slender sclerite in an oblique position, the metaepisternum, which is divided at the upper end by a suture making two divisions in it. Below the metanotum and posterior to the metaepisternum is a sclerite of similar shape, the meta-epimeron (mtem) (Fig. 12). Surrounded by the metaepisternum, the pleurotergite and the meropleurite is the posterior spiracle (spp) (Fig. 17).

There are membranous portions of the thorax near the base of the wings, which allow freedom of movement of parts. There are four small plates or sclerites in this membranous portion, two at the base of the wings, and two posterior and above the ptero-pleurite. The first two are the basal plates (bpl) and the latter are the sub-alar plates (sapl). Above the sub-alar plates is a triangular, more or less distinct, region extending towards the scutellum, known as the juxtascutellum or scutellar bridge. (jscl).

The chaetotaxy of the pleura is similar in both sexes with the exception of the sternopleurite. The anepisternum has four stout bristles near its posterior margin and a more or less covering of hair. In the male, the sternopleurite has one strong bristle below the sternopleural suture, one at the posterior angle of the pleural suture, and one just below the last, also along the pleural suture. (Fig. 12). In the females the last mentioned bristle is wanting. In both sexes the sternopleurite has two (more or less strong) bristles on the anterior surface just above the front coxae, and is somewhat covered with hair on the posterior portion, which become bristles just in front of the mesocoxæ. The coxal sclerite next to the sternopleurite has a row of four strong bristles.

Each spiracle is surrounded by fine hairs which curve over the openings and serve as a protection or sieve.

THORACIC APPENDAGES.

The wings show no difference of structure in the two sexes. (Fig. 13). The costal vein extends to the tip of the fourth vein, and is weakly pectinate. At the tip of the auxiliary vein, the costa is broken, and a short, weak spine is located at the basal

side of the break. The first vein (v1) ends in the costa at about the center of the anterior margin. The second vein (v2) ends by a short, but distinct, curve forward in the costa near the tip of the wing. The third vein (v3) ends at the tip of the wing with a slight curve forward, while the fourth vein, ends either straight or with a slight convergence from the third vein. The anterior cross (acrv) vein meets the margin of the discal cell (dcl) at the distal third, and almost at right angles to the third vein. The posterior cross vein (perv) is oblique, meeting the fifth vein about one-fifth of the distance from the wing margin. The second basal (bcl2) and anal (acl) cells are of equal size and small. The alula (ala) is slightly smaller in the female wing than in the male, but conspicuous in both sexes.

At the base of the costal vein there are two scales (Figs. 13 and 14) which have been called the tegulæ, or epaulets. These lie over the base of the vein, the uppermost one being the tegula or epaulet (ept) and the lower one the sub-tegula or sub-epaulet (sept). These are of some use in the classification of some flies and could probably be used in the Anthomyidae.

The base of the first vein seems to be in three sections. The first two of these have several small openings (Figs. 13 and 15). According to Lowne, these openings, especially the group on the remigium (rm), or first section of the vein, are the chordotonal organs, the same as are found more highly developed in the haltere. Similar openings are also found on the auxiliary vein, at the tip of the first vein, at the tip of the second vein, at the tip of the fifth vein, and on the anterior cross vein (Fig. 13). The membranous portion of the wing is covered with fine spines as are also the veins. The border of the wing has a short fringe of fine hairs.

The squamæ (Fig. 16) are two membranous scales located at the base of and below the wings. When the wing is pulled forward the two scales are plainly seen, the upper or antisquama (sqa) being the anterior and the squama (sq) or lower one, the posterior scale. In this species the antisquama is larger than the squama and round, while the latter is roughly triangular. There is a fringe of long fine yellow hair on each scale, which seems to arise from a thickened border of the membrane. (Fig. 18).

The halteres or balancers are located on the metanotum and according to Lowne they are highly specialized organs of sense.

Though they appear to be rudimentary wings they are far from being vestigial organs. There are three parts, the scabellum (scm), or base, the scape or stalk (sce), and the head (hd) or the apical end (Fig. 11). The halteres are considered to be auditory organs and they carry a fluid in canals similar to the semi-circular canal of the higher animals, giving them the function of maintaining equilibrium.

The three pairs of legs are similar in structure and show slight sex differences. The main difference, which appears in all the legs, is that the bristles and spines of the male are stronger than those of the female. For the purposes of this paper, the legs will be spoken of as if they were drawn out at right angles to the body (Fig. 30). The surface which is then directed forward will be the anterior surface and opposite to it, the posterior surface. That surface which is above will be the dorsal surface and that opposite, the ventral surface.

In the prothoracic legs (Fig. 30A) the coxa (cx) in both sexes is longer than wide, of a somewhat irregular shape, and equipped with five stout spines on the dorsal or flexor surface. (Fig. 21A). The trochanter is small, somewhat triangular, and has no spines, and only one or two small hairs. (Fig. 24A and B). The femur (fm) of the male differs from that of the female in being strongly bowed. In both sexes this segment tapers slightly towards each end, and is armed with rows of strong spines on the posterior surface, two rows especially on the dorsal and ventral margins of the posterior surface (Fig. 28A). The anterior surface of the femur has a few irregular rows of small hairs. The tibia (ti) is as long as the femur, small at the base and slightly enlarged at the apex. (Fig. 31). In both sexes the tibia is armed with a pre-apical bristle and an apical spur. The tarsi (ts) are five-jointed (Fig. 36), the first being the longest and equipped with a distinct spine at its base and smaller ones below that on the ventral surface. (Fig. 36B). All the tarsal joints are pubescent and each of the first four has a weak apical spur (Fig. 36B). The fifth tarsal joint bears two stout, simple claws (clw), two pulvilli (pv), which are larger in the male than in the female (Fig. 34A and B), and a fine hair-like empodium (emp) (Figs. 35 and 36B and C). The tarsi of all three pairs of legs are similar, having no distinct differences. The pulvilli are membranous and covered with long, fine hairs which arise from conical protuberances on the

surface. (Fig. 36E). The tarsal joints are movable, being rather on the order of a ball and socket joint, the attachment between the first two allowing only limited movement (Fig. 36D), and one like that between the fourth and fifth allowing extreme freedom (Fig. 36F).

The mesothoracic legs (Fig. 30B) are the longest of the legs. The coxa (Fig. 20) is roughly diamond-shaped and flattened in a dorsal view, but as viewed anteriorly it consists of two halves. The dorsal half has four or five stout bristles on the dorsal margin of the anterior surface. The trochanter is roughly triangular with a coronet of hairs near the apex (Fig. 23A and B). The femur (Fig. 27) is long, tapering slightly at either end. There are eight strong bristles on the anterior surface, while the rest of the femur is covered with fine short hairs, except at the apex where there are two bristles. The tibia (Fig. 26) is slender, enlarging at its distal end. It is armed with two or three stout spines on its anterior surface, a pre-apical bristle and an apical spur.

The metathoracic legs (Fig. 30C) are of medium length in the male and as long as the mesothoracic legs in the female. The coxa (Fig. 19) is an irregular-shaped piece with one small, stout bristle on the dorsal surface and a row of small bristles on the distal margin. (Fig. 19B). The trochanter (Fig. 22) is somewhat irregular with a strong bristle on its ventral surface. The femur (Fig. 25) enlarges suddenly at the base and tapers slightly at its distal end. Starting at the base, at the dorsal angle, there is a row of stout bristles which curves irregularly on the anterior surface, ending near the apex. There is a row of five fairly stout bristles on the ventral surface. The tibia tapers slightly at the base and besides three strong bristles on the dorsal surface and two on the anterior and ventral surfaces, each, it is armed with a pre-apical bristle and an apical spur. All parts of the legs with the exception of the coxae and trochanters are covered with rather coarse pubescence, or fine hairs arranged in more or less regular rows.

THE ABDOMEN.

When viewed dorsally, the abdomen appears to be composed of but four segments in the female and five in the male. There is, however, an imperfect suture which separates the first and second segments dorsally, and a plate which indicates the first segment as being distinct from the second ventrally.

The male abdomen (Figs. 37 and 38) differs from the female abdomen (Figs. 40 and 41) in shape, number of segments and form of the ventral plates. In general shape it is oval, the anterior end produced laterally, the posterior end blunt. It is about twice as long as broad and the segments, with the exception of the first and last, are of about equal widths. The female abdomen is about the same size as that of the male, but more pointed posteriorly, the second and fifth segments being the longest. The genital segments are barely visible in both sexes from above, and what appears to be the sixth segment in the male is the first genital segment. This is more apparent from the ventral view. Spiracles (sp) are visible on all five segments when viewed ventrally.

Ventrally the first segment is indicated by a short, wide ventral plate (vpl) connected to the dorsal sclerite by a membrane, the abdominal pleura. The second segment is produced into a ring at its anterior margin. The third and fourth ventral plates in both sexes are simple, rather long, and narrowed slightly posteriorly in the female, but almost square in the male. The fifth ventral plate (vp5) in the female resembles the third and fourth, but the fifth ventral plate of the male is complicated, being produced posteriorly into two long branches between which the forceps and genitalia lie when extended.

There are two genital segments in the male, the first a convex, somewhat ringlike segment, and the second (Fig. 37) is almost completely divided into two lateral halves with the anal opening (ao) between them. From the apical margin two branches project which are the forceps. The genital organs are found in the two genital segments but mostly in the second (Fig. 32). At the posterior basal portion of the penis (pns) there is a hooklike process, the posterior clasper (cp) (Fig. 33). Opposite to this on the anterior side is located the anterior clasper (ca).

There is only one genital segment in the female, a small, ring-like segment, with an opening on its ventral surface, which serves as a genital and excretory opening. The genitalia are all internal.

For the most part the abdomen in both sexes is covered with hair, which is shorter and less dense along the median dorsal line. The first segment in the female has no distinct bristles, while the same segment in the male has a few bristles

along the posterior margin. All the rest of the segments have marginal bristles, those at the sides being longer and stronger than those near the median line. The ventral plates have only a few bristles at the margins and a sparse covering of hair towards the center. (Figs. 37 and 40). The first genital segment in the male has several long, strong bristles, while the second has a few along the posterior border. The forceps (fc) each have a distinct spur or tooth near the tip, and are covered with short bristles. The apical point of the second genital segment has two long, weak bristles (Fig. 37). The genital segment in the female has only a few short bristles on the ventral side (Fig. 40).

The chætotaxy of the abdomen is not constant, and the number of marginal bristles varies with the individual.

SUMMARY.

The head, with the exception of the face, the epicephalon and metacephalon, is apparently all one piece, divided into regions which are constant for both sexes. With the exception of the face, the anterior portion of the head is one piece, divided into distinct regions.

The chætotaxy of the head is constant for each sex and can be relied upon.

The thoracic sclerites in the two sexes are the same, and are constant.

The bristles of the mesonotum are constant with the exception of the weak acrostichal bristles which vary in number and arrangement.

The males are always equipped with three sternopleural bristles while the females have only two.

The hair covering of the pleural sclerites is the same in both, but not regular.

The third and fourth veins of the wings are either parallel or diverging at the tip, never converging, while the anterior cross vein is never perpendicular to the fourth vein, meeting the discal cell at its distal third.

The bristles of the legs are constant in location, but not in number, and an apical spur is present on all the tibia.

The abdomen has five segments, and one or two genital segments. The chætotaxy is not constant.

LIST OF ABBREVIATIONS.

ab.	Abdominal segment according to number.	mtn.	Metanotum.
acl.	Anal cell.	npl.	Notopleural bristles.
acer.	Acrostichal bristles.	npls.	Notopleural suture.
acrv.	Anterior cross vein.	o.	Ocelli.
adcs.	Anterior dorsocentral bristles.	obr.	Ocellar bristles.
ala.	Alula.	ocf.	Occipital foramen.
an.	Antennal joints according to number.	om.	Oral margin.
anf.	Antennal fovea.	ot.	Ocellar triangle.
ans.	Anepisternum.	pal.	Post-alar bristles.
ao.	Anal opening.	pcl.	Posterior cell according to number.
ar.	Arista joints according to number.	pely.	Postalar callosity.
axcl.	Axillary cell.	pcrv.	Posterior cross-vein.
axv.	Auxillary vein.	pd.	Prodorsum.
bel.	Basal cell according to number.	pds.	Posterior dorsocentral bristles.
bpl.	Basal plate.	phm.	Posthumeral bristles.
bsu.	Basal suture.	pisu.	Pleural suture.
bu.	Bucca.	pns.	Penis.
c.	Cheek.	prc.	Paracephalon.
ca.	Anterior claspers.	pres.	Proepisternum.
cav.	Costa.	prf.	Parafrontal plates.
cl.	Costal cell.	prml.	Pronotal lobe.
cw.	Claw.	prs.	Prascutum.
cnd.	Condyles.	prsl.	Presutural bristles.
cp.	Posterior claspers.	prsu.	Paracephalic suture.
ex.	Coxa.	psn.	Prosternum.
dcl.	Discal cell.	ptg.	Pleurotergite.
e.	Compound eye.	ptp.	Pteropleurite.
emp.	Empodium.	pv.	Pulvillus.
ep.	Epistome.	pvbr.	Post-vertical bristles.
epc.	Epicephalon.	pwp.	Pleural wing processes.
epos.	Epioccipital sclerite.	rm.	Remigium.
ept.	Epaulet.	s.	Sella.
f.	Front.	sal.	Supra-alar bristles.
fc.	Forceps.	sapl.	Sub-alar plate.
fla.	Facilia.	sc.	Scutum.
fobr.	Fronto-orbital bristles.	scl.	Subcostal cell.
fsu.	Frontal suture.	see.	Scape of the halter.
ft.	Frontal triangle.	scf.	Scutellum.
g.	Genae.	scla.	Scutellar apical bristles.
gn.	Genital segment according to number.	scm.	Scabellum of the halter.
go.	Genital opening.	sept.	Subepaulet.
hely.	Humeral callosity.	smcl.	Submarginal cell.
hd.	Head of halter.	so.	Sensory opening.
hr.	Halter.	sp.	Spiracle.
hum.	Humeral bristles.	spa.	Anterior thoracic spiracle.
ial.	Intra-alar bristles.	spp.	Posterior thoracic spiracle.
jscl.	Juxtascutellum.	sq.	Squama.
l.	Lunule.	sqa.	Antisquama.
mcl.	Marginal cell.	sqd.	Squamoid scale of the halter.
mdtg.	Mediotergite.	ssu.	Sternopleural suture.
merp.	Meropleurite.	stp.	Sternopleurite.
metc.	Metacephalon.	stpbr.	Sternopleural bristles.
metrm.	Meta-epimeron.	tpm.	Tympanic membrane.
metes.	Meta-episternum.	v.	Longitudinal vein according to number.
		vbr.	Vibrissae.
		vcbr.	Vertical cephalic bristles.

EXPLANATION OF PLATES.

PLATE XVII.

Fig. 1. Anterior view of female head.
 Fig. 2. Anterior view of male head.
 Fig. 3. Lateral view of female head, right side.
 Fig. 4. Lateral view of male head, right side.
 Fig. 5. Facc, a facial sclerite which bears the antennæ.
 Fig. 6. Antenna, showing joints and sensoria.
 Fig. 7. Posterior view of male head.
 Fig. 8. Antennal arista.

PLATE XVIII.

Fig. 9. Dorsal view of thorax of male.
 Fig. 10. Anterior view of prothorax of male.
 Fig. 11. Halter.
 Fig. 12. Lateral view of male thorax, right side.

PLATE XIX.

Fig. 13. Wing of male, right wing.
 Fig. 14. Epaulet, sub-epaulet, and base of the costa, of the right wing.
 Fig. 15. Remigium, of right wing of a male, showing chordonotal organs.
 Fig. 16. Left side of male to show squamae.
 Fig. 17. Posterior spiracle of male.
 Fig. 18. Edge of squama.

PLATE XX.

(Legs taken from the right side of male.)

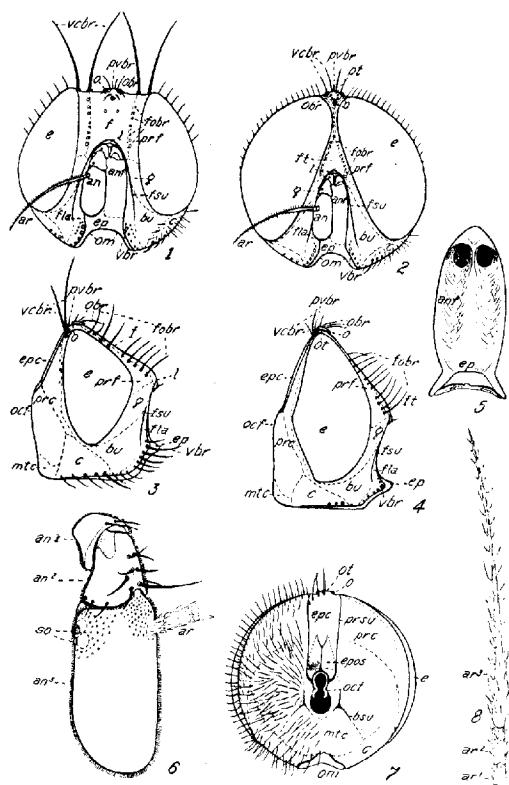
Fig. 19. Metathoracic coxae of male. A, Dorsal view. B, Anterior view.
 Fig. 20. Mesothoracic coxae of male. Dorsal view.
 Fig. 21. Prothoracic coxae of male. A, Dorsal view. B, Anterior view.
 Fig. 22. Anterior view metathoracic trochanter.
 Fig. 23. Mesothoracic trochanter. A, Anterior view. B, Dorsal.
 Fig. 24. Prothoracic trochanter. A, Posterior view. B, Ventral.
 Fig. 25. Metathoracic femur, dorsal view.
 Fig. 26. Mesothoracic tibia, anterior view.
 Fig. 27. Mesothoracic femur, dorsal view.
 Fig. 28. Prothoracic femur. A, Posterior view. B, Dorsal view.
 Fig. 29. Mesothoracic tibia, dorsal.
 Fig. 30. Anterior view of legs in position as described. A, Prothoracic, B, Mesothoracic. C, Metathoracic.
 Fig. 31. Prothoracic tibia, posterior view.

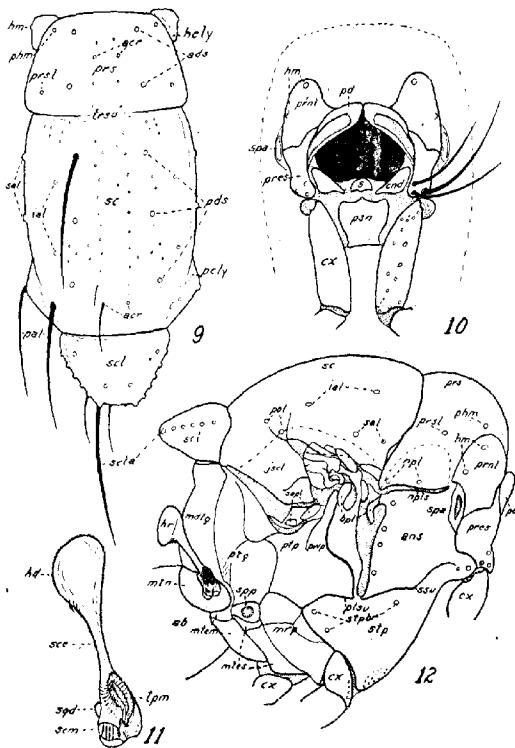
PLATE XXI.

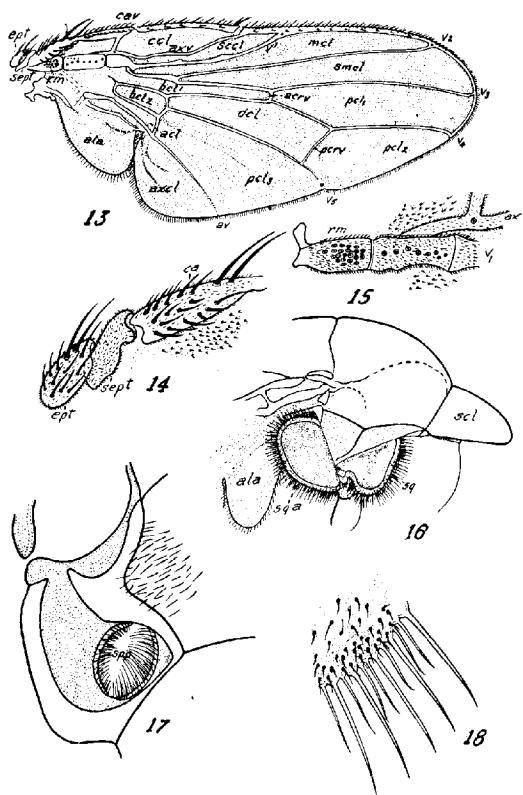
Fig. 32. Second genital segment and genitalia of the male.
 Fig. 33. Genitalia with genital segment and forceps removed.
 Fig. 34. Pulvilli. A, Male. B, Female.
 Fig. 35. Apex of last tarsal joint of male, posterior view.
 Fig. 36. Tarsus. A, Dorsal view of first joint, (outline). B, Posterior view of all tarsal joints. C, Dorsal view of last two tarsal joints. D, Union and articulation between first two tarsal joints. E, Edge of pulvillus showing roughened surface. F, Union and articulation of last two tarsal joints.

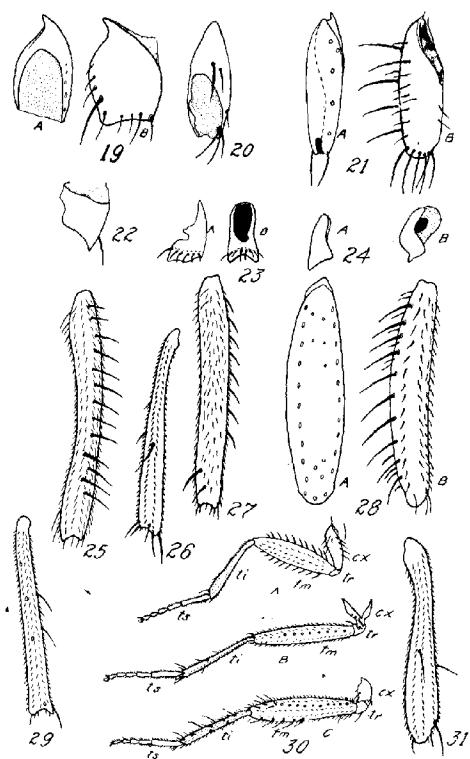
PLATE XXII.

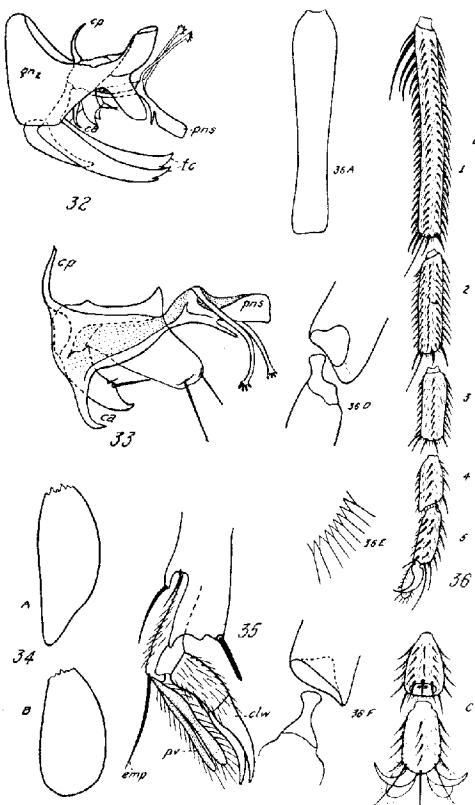
Fig. 37. Ventral view of male abdomen.
 Fig. 38. Dorsal view of male abdomen.
 Fig. 39. Section of abdominal wall to show flexibility of segments.
 Fig. 40. Ventral view of female abdomen.
 Fig. 41. Dorsal view of female abdomen.

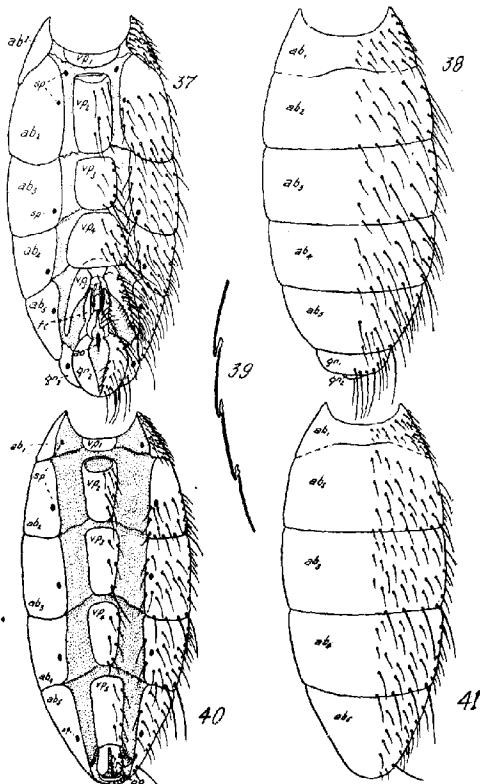












THE DIGESTIVE SYSTEM OF THE PERIODICAL CICADA, TIBICEN SEPTENDECIM LINN.

L. M. HICKERNELL, Syracuse University.

I. Morphology of the System in the Adult Insect.

- I. Introduction.
- II. Literature.
- III. Material and Methods.
- IV. The Digestive Tube of the Adult Male Insect.
- V. Relative Conditions in Male and Female.
- VI. Discussion.
- VII. Summary and Conclusions.
- VIII. Bibliography.
- IX. Description of Figures.

I. INTRODUCTION.

Numerous authors have reported the impossibility of following the digestive system of the periodical cicada throughout its entire length. Of those who state that it is complete and well organized, none attempts any detailed description. My attention was called to the matter in 1916 by Dr. C. W. Hargitt who had himself been interested in the question of digestive activity in this insect for some years. Dr. Hargitt's observation dealt particularly with the feeding habits of the cicada. He had also directed a graduate student, R. L. Henderson, in an attempt to work out the morphological details of the enteron. Unfortunately before this work was completed the death of Mr. Henderson intervened.

In the present work I have constantly consulted with Dr. Hargitt, but the entire responsibility for the morphological details herein presented lies with me. A further publication, in which Dr. Hargitt has the major interest, dealing with the physiological aspects of the problem, will appear shortly.

II. LITERATURE.

There has been much lack of agreement in the literature as to whether the cicadas do or do not feed and this question has led in turn to the inquiry as to whether the digestive tube is atrophied in the supposed cases of non-feeding. Marlatt (1898) in his summary of the habits of the insect, says that during its aerial existence "it seldom, if ever, takes food." In

another place he says that feeding is limited to the female, the digestive system of the male being rudimentary.

Quaintance (1902) made a series of careful observations upon the brood which emerged in Maryland during the early summer of 1902. He was able to find numerous insects, both male and female, apparently feeding upon the branches of young fruit trees. He snipped off an insect's proboscis while the latter was embedded in the bark of a twig and shows a photograph of a section of this bark pierced by the setæ. He states that he found that the alimentary tract was not rudimentary in either sex, although he attempts no description nor gives any figures to prove his statement.

Hargitt (1903) suggested that there seems to be a complete atrophy of the hind gut at the time of emergence while the mid-gut undergoes an increase in size until the abdomen is almost entirely hollow. He suggests that this condition represents an adaptation enabling the insect to make use of the stored fat, using this food to the exclusion of plant juices.

Marlatt (1907) in a revision of his earlier bulletin corrects his former statements regarding the feeding habits of the cicada. He is convinced of the possibility of feeding by the observation of Quaintance, but still questions whether the cicada necessarily takes food.

In an unpublished paper by R. L. Henderson, under the direction of Dr. Hargitt, to which we have had access, numerous observations were recorded which have proven valuable in this study. Although Henderson did not work out the digestive system completely, his account shows that he had identified and traced the course of certain parts of the canal.

Dufour ('33) describes and figures the digestive system of *Cicada orni*. In general his findings are very similar to those here presented for *Tibicen septendecim*, except that he did not recognize the complication of crop and "internal gland." According to Dufour the esophagus dilates posteriorly to make the crop. The crop continues into the "poche du ventricule chylifique." Then follows a smaller much-coiled tube which finally runs forward, apparently emptying into the anterior portion of the "ventricule chylifique." The crop gives off a lateral diverticulum which continues posteriorly as a narrow, much-coiled tube and finally empties into a short rectal division which ends at the anal opening.

From the above it is evident that there is no agreement as to the necessity of feeding in the adult insect nor has the morphology of the digestive system been worked out sufficiently, in *Tibicen septendecim* or any closely related forms, to warrant inferences as to functional activity based upon structural conditions.

III. MATERIAL AND METHODS.

The observations herein recorded are based upon the periodical cicada, *Tibicen septendecim* Linn. Numerous specimens of the so-called dwarf cicada have been collected, but they were not used in this work. Material was collected during June, 1916, by the author in the vicinity of Syracuse. Additional insects were gathered near Moores Hill, Indiana, by Dr. A. J. Bigney.

The material was fixed in the following fluids: Bouin, 10% formol, sublimate acetic, Gilson, potassium dichromate, and Zenker. In order to insure rapid penetration of the fluids, the integument was slit with a razor on the ventral side, or the head was cut off allowing the fluids to penetrate rapidly from the anterior end.

Dissections of freshly killed and also of preserved insects were made under the binocular microscope. The dissection method was not sufficient to reveal all of the relationships of the digestive organs so that serial sections of entire insects, as well as of parts of the digestive tube with adhering tissue, were made.

In making serial sections of entire insects it was necessary to soften the chitinous integument by means of Labarque's solution. After this process the insects were embedded by the double method of Apathy and sections were cut ten microns thick. Such sections were valuable only for determination of general topographical relationships.

The various digestive organs were dissected out and serial paraffine sections 5 microns thick were made in the usual manner. They were stained with hematoxylin and eosin. By means of these sections various relationships were made apparent which could not be cleared up by gross dissections.

IV. THE DIGESTIVE TUBE IN THE ADULT MALE INSECT.

The male has been chosen as the subject for more detailed description because of the fact that in this sex particularly more doubt has been expressed as to the completeness of the enteric canal.

In the cicada it is difficult to recognize the boundaries of the fore, mid and hind guts. Not only do these parts fail to conform in their gross anatomy to the relatively simple divisions as found, for example, among the Orthoptera, but their histological structure also fails in most cases to correspond with that of the more familiar forms. The puzzling relationship of parts and the changes taking place in some of these parts during the life cycle may be due to any or all of several factors, viz., the nature of the liquid food; the influence of food stored in the body in the form of fat; or to the peculiar life history of the insect. However, since most of the sap-sucking Hemiptera in which the digestive apparatus has been described have some similar peculiarities, no clue is obtainable from them as to the significance of these conditions. That part of the following description relating to the sequence of parts in the tube and to their general relationships can best be understood by reference to Fig. 3. This is entirely schematic and attempts to represent none of the finer details of structure.

The extreme anterior portion of the digestive canal is not greatly different from that described for numerous other forms. The long proboscis, containing a pair each of functional stylet-like mandibles and maxillæ, leads dorsally through the pharynx into the narrow esophagus. The latter, when it reaches a point midway between the dorsal and ventral surfaces of the animal, turns at right angles and proceeds toward the posterior end. The point where the esophagus changes direction is just posterior to the boundary between the head and prothorax.

The esophagus does not vary much in diameter throughout its entire extent, (Figs. 2 and 3). It may, with little difficulty, be followed in a properly dissected specimen, with the unaided eye, and it is easily traced with a lens of low magnification. At the line of division between the mesothorax and the metathorax the esophagus empties into the crop.

The crop is divided into two parts of unequal size. The anterior part (Figs. 1, 2 and 3, ac) is the smaller and is usually

confined to the metathorax. The posterior portion (Figs. 1, 2 and 3, pc) has its anterior boundary at the beginning of the first abdominal segment. Its extent in the posterior direction is variable and this variation will be discussed later but in extreme cases its posterior boundary is found as far back as the sixth abdominal segment.

The dorsal wall of the anterior crop is concealed by a winding mass of tubes which will be described later. For want of a better name this mass will be called the "internal gland," following the terminology of Lubbock ('59). Although Lubbock probably intended his designation to include more than it does in the present case, it seems expedient to continue the use of the term in connection with that part of the complex made by the ascending intestine and malpighian vessels just above the anterior crop. In shape, this complex of crop and internal gland usually appears as an elongated spheroid, but it may be bent upwards so as to look in side view like an inverted U. The diameter of the entire structure is roughly five times that of the esophagus. Posteriorly it narrows and apparently connects with the large posterior crop.

The descending intestine arises from the left side of the internal gland near its anterior margin. In a gross dissection this tube sometimes appears to be a continuation of the esophagus but sections of this region show it to be otherwise, as will be explained later. It is only about half the diameter of the esophagus and is characterized by a gray color which is uniform throughout its whole extent. It follows the ventral margin of the anterior crop but leads in a general posterior direction. The windings of this tube are confined in most cases to the dorsal half of the insect. At the boundary between the sixth and seventh abdominal segments it winds upon itself in such a way as to make a knot (Figs. 1, 2 and 3, kk). From this knot or coil the tube emerges and joins the rectum which latter narrows as it passes posteriorly until it ends in the anal opening.

The posterior end of the internal gland receives another tube (Figs. 1, 2 and 3, at) which is distinguishable from the one previously described both as to its color and also with regard to the course it takes. Its color is noticeably yellow, a condition as will be shown later, traceable to the presence of cytoplasmic inclusions in the epithelium of its walls. This yellow tube, the ascending intestine, also runs in a sinuous fashion over the sur-

face of the posterior crop but is chiefly confined to its ventral surface. Following the intestine backward it may be traced to the posterior boundary of the sixth abdominal segment where it takes a dorsal course toward the rectum. As in the case of the descending intestine, a knot or coil is formed (Figs. 1, 2 and 3, k) but when the tube emerges from the coil, it turns anteriorly and connects with the posterior crop at the extremity of the latter (Figs. 1 and 2, x).

The posterior crop is one of the most puzzling divisions of the tube at first sight. It is enormously developed, especially in the adult male during later life, and its gradual enlargement from the period of emergence to late life is one of the anomalies demanding adequate explanation. Because of the thinness of parts of its walls its true nature might be unsuspected if one depended upon gross dissections alone. In the adult male it extends from the metathorax to the end of the sixth abdominal segment (Figs. 1, 2 and 3, pc). An anterior cæcal prolongation extends forward beneath the crop as indicated in Fig. 3. Its main portion gradually enlarges posteriorly except for indentations at the boundaries of one or two segments until, beginning in the region of the second abdominal segment, its walls closely approximate the chitinous integument on all sides. The small intestinal tubes connecting fore and aft with the internal gland run their courses upon its outer surface as indicated above.

The rectum is confined usually to the last two abdominal segments (Figs. 1, 2, 3, r). It is an elongated sac with numerous longitudinal folds and lies close to the dorsal integument. It is easy to understand how some writers may have gotten the impression that the digestive tube of the male insect did not have any complete posterior portion, for in all cases where a dissection is attempted from the dorsal side the rectum is destroyed. It is practically impossible to remove any part of the dorsal integument in this region without injuring the underlying rectal sac. It can be exposed, however, by carefully dissecting from the ventral side, through the mass of coiled reproductive ducts and fat.

The foregoing description is based entirely upon observations in the adult male insect. While the female organs are arranged on the same general plan, there are slight variations and these will be mentioned in another place.

From what has been said it should be apparent that the adult male cicada possesses a digestive tube which is most peculiar both with respect to elements which compose it and to the manner of their arrangement. It is possible to demonstrate by dissections alone, that this insect has a complete and continuous digestive tube yet this fact has been denied by many, and even when admitted, the arrangement and connections of the organs have been imperfectly understood. The relationships of the various parts described must depend upon the study of sections, for it will shortly appear that certain apparent connections between elements as indicated in whole preparations are indeed apparent and not real.

RELATIONSHIPS OF THE DIGESTIVE ORGANS.

As suggested above, the connection between the various parts of the digestive system are not very clear in gross dissections. The actual union of some of the different divisions of the system can be clearly demonstrated only in sections.

With the view of determining the true nature and relationships of parts in the anterior part of the digestive tube, the crop with the internal gland was dissected out of numerous adult insects. Transverse, sagittal and frontal sections were cut, and by means of these the independence of crop and internal gland was established. A median sagittal section of the anterior part of the tube shows that the esophagus is separated from the crop by a valve and that the anterior crop then continues in a posterior direction. As it proceeds, however, its walls become much modified, the floor being greatly thickened, while the roof is relatively thin and much folded. The folds in the roof are very pronounced and run in a general antero-posterior direction. This condition results in the formation of deep external fissures on the dorsal surface of the anterior crop, the ascending intestine and malpighian vessels each being enveloped by the walls between two adjacent folds. These relationships may be understood by reference to Fig. 9, which is a transverse section through the anterior crop region. The same structures are also represented diagrammatically in Fig. 6.

This modified anterior crop upon reaching the posterior portion joins directly with the latter. The aperture leading into the posterior crop is small and irregular by virtue of the convoluted walls of the connecting portions. While the dorsal

wall of the anterior crop is thin and has its epithelium poorly developed, this does not imply that there is any connection with the tubes which coil above this region. The anterior crop receives no tube, other than the esophagus, nor does it give off outgrowths in any part.

It was stated previously that the descending intestine, arising from the left anterior part of the "internal gland," looks, in a dissection, as if it might be a posterior continuation of the esophagus. Sections do not confirm this possibility. On the contrary, a frontal section (Fig. 7) shows the descending intestine to be continuous with the ascending intestine. The latter enters the internal gland posteriorly and runs forward to its anterior margin. A comparison of sections in three different planes proves, then, that the enlargement in the metathorax is composed of two distinct parts—a dorsal, tubular, closely-wound mass made by the ascending intestine and malpighian vessels, and a ventral distensible portion continuous with the esophagus.

The posterior crop neither receives nor gives off any outgrowths until its extreme posterior end is reached. Sections show (Fig. 14) that it empties directly into the narrow ascending intestine which then proceeds in a general anterior direction to join in the formation of the internal gland, as previously described. A muscular ring or valve is found at the junction of the last mentioned parts.

There are four malpighian vessels. They are easily found in any section between the crop and rectum. They are not easily distinguished in dissections since they are almost the same in color as the fat which surrounds them. Their diameter is about half that of the intestine. The blind ends of the tubules lie in the extreme posterior end of the body. They run forward in irregular fashion, mostly dorsally, until they approach the region of the anterior crop. Here they describe a short loop just above the internal gland and then disappear into it at its posterior margin.

From the foregoing descriptions it is clear that if plant juices are taken in as food, they are conveyed to the anterior crop directly through the esophagus. They then pass to the posterior crop which, in all probability, functions as a storage sac as well as contributing to the digestive process. From the posterior crop the liquid food passes into the ascending

intestine through which it goes anteriorly until it reaches the internal gland. After traversing the latter it again starts in a posterior direction through the descending intestine and finally enters the rectum, the last organ of the system. There seems to be no possibility that the food material takes any other course than that outlined above. There are no connections between the parts described which would permit any other course, and the presence of valves shows that the food stream could follow only the direction outlined.

HISTOLOGICAL STRUCTURE OF THE DIGESTIVE ORGANS.

The Esophagus.

The epithelium of the esophagus has no prominent cell boundaries. Here and there can be seen cells whose free margins are separated by walls, but for the most part the epithelial lining appears as a syncytium. The nuclei are prominent, being large and containing numerous chromatic granules rather evenly scattered. The nuclei do not all lie near the proximal ends of the cells, but appear near the distal border as well.

The cytoplasmic portion shows no differentiation between basal and free ends, but is uniformly made up of fine granules or minute fibrillæ which seem to compose the more solid portion of the cytoplasmic mass. Here and there are found vacuolar spaces within the cytoplasm, but in no place does one find cytoplasmic inclusions which could be considered as evidence of secretion or absorption. The latter statement is based upon observations upon sections from numerous insects of different ages in which a wide variation as to activity in feeding was possible. The free margin of the epithelium is bounded by a definite wall, but there does not appear to be any cuticula or striated border. The epithelium lining the esophagus would seem, from these observations, to have a purely passive function, conducting the food material posteriorly, but not contributing otherwise to the digestive or absorptive processes.

The cells of the esophageal epithelium have a well developed basement membrane. Connective tissue elements thicken this in places (in the middle of the folds, for example) in such a way that the folds seem to have a dense core of darkly staining material in which the details of structure do not show them-

selves plainly. This layer of connective tissue elements may be traced entirely around a transverse section.

Adjoining the basement membrane are found two or three layers of muscles—an inner longitudinal and an outer circular layer. The longitudinal layer is not well developed, but consists of scattered bundles of fibres which fit into irregularities at the bases of the epithelial folds. Each muscle is composed of from one to a dozen fibres. The poor development of this layer would suggest that it has little if any functional importance. The circular layer is better developed. It consists of several strata of striated muscle fibres which interweave, making a network (the individual fibres do not branch), which surrounds the tube. Muscle nuclei are not prominent in the layers, but the fibres are easily seen and studied.

In many parts of transverse sections other groups of longitudinal muscle fibres are found outside the circular layer above described. These are numerous and well developed in contrast to the longitudinal layer lying at the base of the epithelium. Inasmuch as the esophagus lies between the large thoracic muscles which attach to the appendages, it is likely that the last described elements are members of this thoracic muscle mass.

The succession of layers above described corresponds rather closely to that in the esophagus of other insects. There is, therefore, nothing remarkable about this organ in a structural sense.

The lumen of the esophagus is continuous with that of the anterior crop through a narrow passageway running between well-developed epithelial folds. These folds have at their bases circular muscles and much connective tissue. A longitudinal section of this region shows that this arrangement is a real valve with a sphincter. It must, therefore, function in preventing the flow of juices back into the esophagus once they have arrived in the anterior crop cavity. On the esophagus side of the valve the epithelium is not folded but gives a funnel shape to the lumen as it runs posteriorly. On the crop side, however, the epithelial lining is thrown into numerous folds (Fig. 10), especially at the point nearest the actual opening in the valvular structure. Liquid going in the wrong direction would thus be hindered in its progress by the folds and a con-

traction of the sphincter would so close the lumen as to prevent effectively passage of any liquid.

The Anterior Crop.

The esophagus empties into the anterior crop through the narrow opening described above. The walls of this division are not uniformly differentiated (Fig. 9). The floor of the organ is so constructed as to permit little expansion. The roof is much folded, the folds apparently allowing some distension as a result of the pressure of the contained liquid food. These differences of structure are easily observed in either longitudinal or transverse sections.

The epithelium covering the floor of the anterior crop is made up of columnar cells varying somewhat in length. Anteriorly its surface is thrown into a series of gentle folds (Fig. 8). The folds increase in height until in the extreme posterior end they much resemble the gastric crypts of some of the vertebrates. The cell boundaries, easily seen in the distal portions of the cells, become less sharply marked as the base of each cell is approached. The cytoplasm of the cells is uniformly granular or homogeneous. No vacuoles or secretion products were observed. The nuclei are large and chromatic and they may be found in almost any position between the base and free ends of the cells. No cuticula or striated border was observed, the free ends of the cells having membranes similar to those covering the basal portions.

The roof of this division has an epithelium much different in character from that above described. The cells are more cubical than columnar. The dorsal folds are very deep (Fig. 9) while secondary folds branch off from the one or two large primary ones in such a fashion that in transverse section the pattern formed resembles the branches of a tree. There is a pronounced cuticula developed upon the surface of the dorsal epithelium.

Cross sections through any part of the anterior crop region show the ascending intestine and malpighian vessels to be closely apposed to the dorsal wall of this organ. These tubes lie in the depressions between the folds previously described but do not actually penetrate the folds at any point.

The entire mass formed by anterior crop and entwined tubes is covered with a peritoneal membrane together with some muscle fibres. The resulting saccular appearance and the

apparent unity of the structure as viewed externally, together with its likeness to glandular tissue as seen in section accounts for the name "internal gland" applied by other authors. The term is retained here only as a convenient designation and for want of proper name which will suggest its real anatomical or physiological nature.

The passageway between anterior and posterior crop is small and irregular in outline. Both divisions of the crop are much folded in a longitudinal direction at their point of junction. This makes a narrow, tortuous connection, at least when the two parts are not distended with food. The circular muscles in this region are not well developed so that there does not appear to be any valvular apparatus for the separation of the two cavities.

The anterior end of the second division of the crop has its walls much folded. These folds are so close to each other that the lumen is a mere irregular slit. The epithelium in this region is not greatly dissimilar to that found in the floor of the anterior crop. The muscles in the walls of the posterior crop are arranged in an inner circular layer which is thin and evenly disposed, and an outer longitudinal layer whose fibres lie in scattered groups close to the circular layer.

In the anterior portion of the posterior crop the epithelial cells are packed with oval brownish inclusions similar to those found in the ascending intestine, described later.

In the middle portion of the posterior crop the epithelium thins out to such an extent that it forms the thinnest of lining membranes (Figs. 12 and 13). The cells lose their columnar character and become cuboid or even squamous. Cell boundaries are indistinct or entirely lacking. The free border of these cells has a striated zone beneath which is a narrow dense layer of granular cytoplasm followed by colorless alveolar substance which is probably made up of small vacuoles filled with fluid. The proximal portions of the cells are filled with a finely granular protoplasm. The muscle layers are not well developed although they may be demonstrated in certain places.

In the posterior end of the posterior crop the epithelium becomes somewhat thicker, especially so at the point where the ascending intestine connects with it. Here again the cells show the yellow inclusions which look somewhat like oil droplets. These are similar in appearance to those found in the most anterior portion.

The opening from posterior crop into the ascending intestine is surrounded by a sort of transitional epithelium. Here the cells are tall and closely packed. They are thrown into slight folds (Fig. 14) but not to the extent found in some other portions of the digestive epithelium. There is a well-developed layer of circular muscles at the place where the tube arises, presumably a sphincter or valve, guarding the opening into the ascending intestine.

The Ascending Intestine.

The ascending intestine, in histological structure, shows great difference from the parts previously described. The lining of this tube is composed of a single layer of irregular epithelial cells which, when fully developed, are very large (Figs. 15 and 16) and have a prominent, centrally-located nucleus. Of all the digestive epithelia thus far considered, that of the ascending intestine seems to be most active. The cytoplasm at the base of each cell is granular, but as the free end of the cell is approached large globules are developed (Fig. 16). When the globules are not present, vacuoles of varying sizes are found in the protoplasm near the distal ends of the cells (Fig. 15).

The nuclei of the large fully-developed epithelial cells become vacuolated just previous to secretion. At the bases of the larger cells are found numerous small replacement nuclei which suggest the method by which new cells are formed to take the place of those cast off. In Fig. 17 the lighter colored cells are apparently in process of developing to replace those destroyed by secretory activity, while the darker ones are about to secrete. The free margin of the cells is bounded by a well-developed striated border. This is so prominent that at certain times it gives the cells the appearance of being clothed with short cilia.

The epithelial cells lining the entire tube from its place of origin to the point where it goes into the internal gland show signs of functional activity of the sort above mentioned. Figs. 15, 16 and 17 represent different phases of the secretory process.

At the base of the epithelial layer is a thin stratum of circular muscle fibres. In some places this is hard to distinguish from the basement membrane of the epithelial cells.

Just outside of the circular muscle layer scattered bundles of long muscle fibres are found. This incomplete long muscle layer is not different in character from that described for the anterior crop.

The Malpighian Tubules.

The walls of the Malpighian tubules are made up of a single layer of cuboid cells. The nuclei of these cells are large and sometimes irregular. The cytoplasm is granular or alveolar depending upon the phase of the secretion process. A well developed intima is present in the cells. In certain places a tubule may be made up of enormous cells placed end to end, in which case there is a single large intracellular duct into which drain numerous smaller ducts which ramify in the cytoplasm in a lateral direction.

At the point where the tubules enter the "internal gland" there is an abrupt change in the character of their walls. They become thin, the nuclei decrease in size and are less chromatic. They retain this membranous character until they finally empty into the intestine near the anterior margin of the "internal gland," at the junction of the ascending and descending intestine.

The "Internal Gland."

As previously explained, the name "internal gland" was used by Lubbock in 1859 to denote the closely wound knot formed by a part of the digestive tube in the thoracic region of certain Hemiptera. The term is here used to designate the complex formed by the ascending intestine and malpighian vessels dorsal to the anterior crop.

The ascending intestine, after running almost the entire length of the abdominal cavity, in the manner previously described, begins a series of coils just above and closely apposed to the dorsal wall of the anterior crop (Fig. 3). Immediately before entering this coil the diameter of the tube becomes somewhat enlarged and there appears to be much secretory activity on the part of the cells of its epithelial lining for they are much vacuolated both as to cytoplasm and nuclei and the free ends of the cells become cast off into the lumen to a greater extent than in the cells nearer the end where the tube originates.

The tube then becomes closely wound upon itself and as it proceeds forward lies close to the wall of the anterior crop. Signs of functional activity are not as pronounced as the tube is followed forward. The cells contain few or no secretion bodies or vacuoles. Cell particles also cease to be cast into the lumen of the tube.

The malpighian tubules accompany the ascending intestine forward contributing a large percentage of the mass of the "internal gland." Their walls become extremely thin while the lumen of each vessel increases greatly in size. These conditions are represented in Figs. 7 and 9 mt.

The Descending Intestine.

While the ascending intestine emerges from the internal gland its epithelium becomes markedly changed. The cells are low and flat and contain no cytoplasmic inclusions. As the tube leads posteriorly the epithelial lining takes a transitional form. This point marks the entrance of the malpighian vessels and the junction of the two intestinal divisions.

The descending intestine is lined with a single layer of large epithelial cells. Anteriorly these cells are vacuolated (Fig. 18), but in the middle and posterior parts the cytoplasm is uniformly granular (Fig. 19). The lumen of the tube is irregular in outline by reason of the triangular shape of the limiting cells. These cells are bordered by a zone of cytoplasm much denser than that found centrally. This dense peripheral zone is distinguishable in the basal parts of the cells next to the underlying muscles as well as at their free borders. This condition reminds one strongly of the ectoplasmic and endoplasmic zones in protozoa.

The nuclei of these cells are large and centrally placed and contain many coarse chromatic granules. Nucleoli do not appear nor are the nuclei vacuolated as was the case in the ascending intestine. The cytoplasm surrounding the nucleus is finely granular or fibrillar, except in the region immediately following the emergence from the internal gland (Fig. 18). Here both cytoplasm and nucleus may show vacuoles. It is to be noted that here also the vacuolation is not accompanied by the modification of the outer zone of protoplasm as previously described.

A comparison of sections of the ascending and descending intestine shows that their color is due to the histological structure of the cytoplasm in each case, the yellow color of the former being caused by the numerous inclusions. The complete absence of these in the descending intestine results in a color difference which enables one to recognize this tube with the naked eye.

The Rectum.

The rectum is relatively short and its diameter is much greater than that of any part discussed thus far except the posterior crop. Its walls are also much thicker than those of any other part of the digestive tube. The epithelial lining is similar to the esophageal epithelium in that the columnar cells are narrow, closely packed, thrown into numerous small folds, and the cell boundaries are indistinct. The muscle layers do not have their fibres running in strict longitudinal and transverse directions, but there are many strands of muscle material running in criss-cross fashion so that a sort of woven mat of tissues makes up the muscular part of the rectal walls. In places, however, distinct layers may be seen, an inner thin longitudinal layer and an outer thick circular layer. The muscle is of the striated variety in both layers and is gathered into typical bundles. The great thickening of the circular layer is not surprising in view of the functional activity of this layer in emptying the rectal cavity.

V: RELATIVE CONDITIONS IN MALE AND FEMALE.

The different divisions of the digestive tube in the female adult do not differ greatly from those described in detail for the male. The gross and microscopic arrangement of parts is the same in general plan. Esophagus and anterior crop are practically identical in structure in the two sexes. The posterior crop is much smaller in diameter in the female, its walls being crowded together by the surrounding fat and reproductive organs, but the walls themselves are similar in structure to those of the male. Ascending and descending intestine and rectum show no structural differences in the two sexes. There is, then, no great difference in the general plan and arrangement of the digestive organs of the male and female.

A gradual increase in the size of the posterior crop during the adult life of the cicada is noticeable. This increase in size is accompanied by a corresponding gradual decrease in the volume of the fat body. This results in the cavernous abdomen of the adult in its final period of existence, a condition especially striking in the male, but also observable in the female during its later history. Since the space necessary for the accommodation of the eggs is much larger than that required to store the sperms, this may account in part for the smaller average size to which the posterior crop attains in the female.

VI. DISCUSSION.

The relationship of parts in the digestive system of *Cicada orni*, as described by Dufour ('33), is unintelligible when the gross anatomy of the organs are alone considered. On the basis of what we have found in sections of the same system in *Tibicen septendecim*, however, it seems easy to homologize the structures described by Dufour with the corresponding ones in the present subject and to suggest further that the two much-coiled portions of the intestine figured for *C. orni* are connected by a labyrinth similar to the one described here as the "internal gland." Dufour did not study sections of his material and ordinary dissection methods would not reveal the relationships which are made plain by sections. If, in *C. orni*, there is any difference between the digestive systems of male and female, Dufour's figure is undoubtedly that of a female specimen. At any rate, the digestive apparatus is nearly identical with that of a female *Tibicen septendecim*. The one slight variation, namely, the point of connection between the ascending intestine and "internal gland," is easily explainable since the anterior portion of the posterior crop is usually much folded in these forms and the ascending intestine might be so placed between folds, and perhaps in addition have its wall actually grown fast to those of the ascending intestine, so as to appear to empty into the "ventricule chylifique" (posterior crop). Examination of Dufour's figure of the digestive system of *Cicada orni* after studying sections of the same in *Tibicen septendecim* does not leave much doubt as to the similarity of the digestive apparatus in the two species.

VII. SUMMARY AND CONCLUSIONS.

1. There is a well-differentiated and continuous digestive tube in both male and female adult *Tibicen septendecim*.
2. The esophagus, which empties into the crop, shows no peculiarities of structure.
3. The crop is divided into two unequal parts (the anterior and posterior crops) by a constriction at the place where thorax and abdomen join.
4. The crop is partially obscured by a mass made up of ascending intestine and malpighian vessels. This mass has been called the "internal gland" (Lubbock '59).
5. The posterior crop is greatly enlarged, especially in the adult male, and its epithelium is extremely thin except at the extreme anterior and posterior ends.
6. The posterior crop empties into the ascending intestine which is yellow in color and runs forward until immediately dorsal to the anterior crop it winds about with the malpighian vessels to make the "internal gland."
7. The ascending intestine emerges from the internal gland and empties into the descending intestine.
8. The malpighian vessels are four in number and they empty into the digestive tube at the junction of ascending and descending intestines.
9. The descending intestine runs dorsally in a general posterior direction until it joins the rectum. The former is gray in color.
10. There is no degeneration of parts of the digestive tube of either male or female in the sense that any part ceases to be well organized or becomes disconnected from another part.
11. Nothing has been learned in connection with this study which throws any light upon the reasons for the peculiar life history of the cicada.

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IX. INDEX TO FIGURES.

ac—anterior crop.
at—ascending intestine.
cm—circular muscles.
dt—descending intestine.
e—esophagus.
int—internal gland.
k—coil in ascending intestine.
kk—coil in descending intestine.
mt—malpighian vessels.
pc—posterior crop.
r—rectum.
x—junction of posterior crop with ascending intestine.
y—junction of malpighian vessel and intestine.

EXPLANATION OF PLATES.

PLATE XXIII.

Fig. 1. Semidiagrammatic representation of ventral aspect of digestive system based upon dissections and reconstructions from sections. 10X.
Fig. 2. The same viewed from the left side.

PLATE XXIV.

Fig. 3. Diagram of the digestive organs showing the relationships of the various parts and the course of the food stream.
Figs. 4, 5, 6. Diagrammatic figures of cross sections in anterior crop region showing probable method of complication resulting in intimate relation between anterior crop and "internal gland." Cf. Figs. 6 and 9.

PLATE XXV.

Fig. 7. Frontal section through internal gland and anterior part of descending intestine.
Fig. 8. Vertical section through floor of anterior crop.
Fig. 9. Transverse section through forward part of internal gland, anterior crop and descending intestine.

PLATE XXVI.

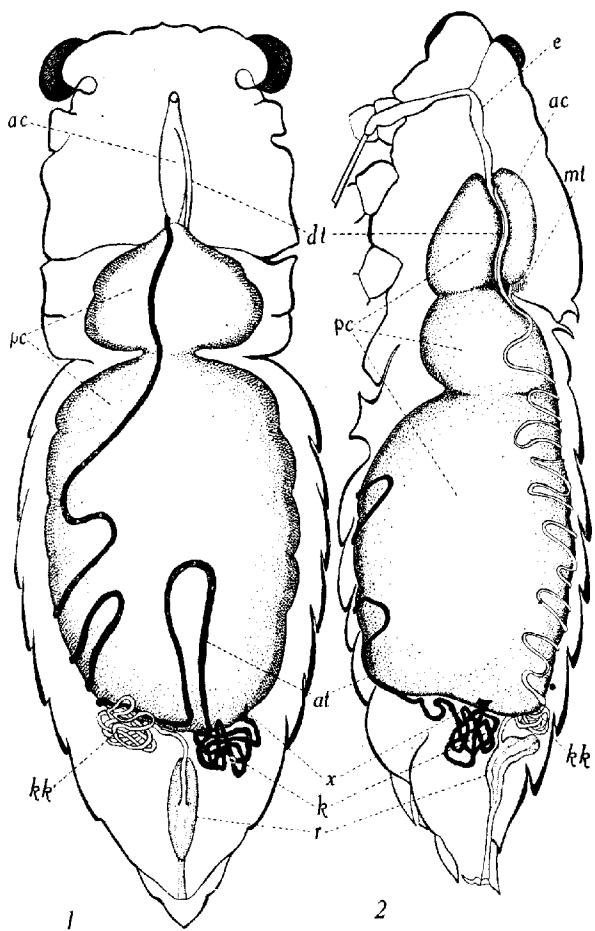
Fig. 10. Sagittal section showing junction of esophagus with anterior crop.
Fig. 11. Section through extreme anterior portion of posterior crop showing details of cell structure.
Fig. 12. Same slightly posterior to Fig. 11.
Fig. 13. Same midway between extremities of posterior crop.

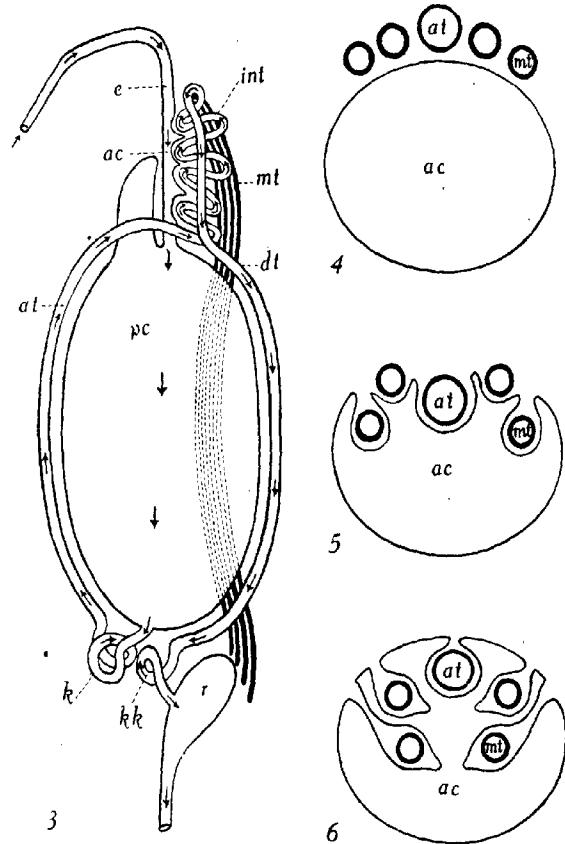
PLATE XXVII.

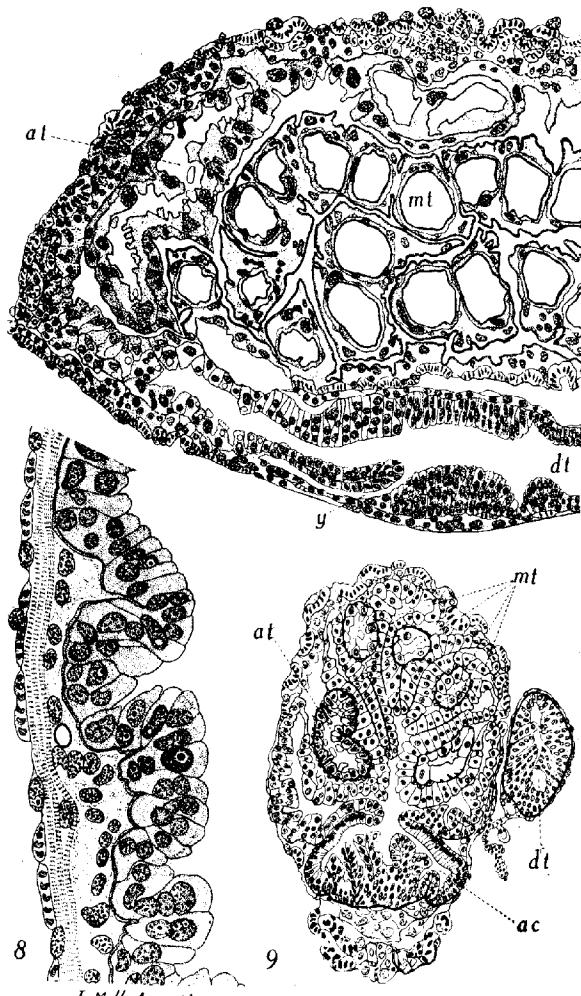
Fig. 14. Section showing junction of posterior crop and ascending intestine.
Figs. 15, 16, 17. Transverse sections through different parts of ascending intestine showing different phases of digestive activity.

PLATE XXVIII.

Fig. 18. Transverse section through descending intestine at its anterior end.
Fig. 19. Same, midway between its extremities.







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